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Hamiltonichthys mapesi, g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas

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ABSTRACT

A new genus and species of hybodontiform elasmobranch, *Hamiltonichthys mapesi*, is described on the basis of six specimens from the Upper Pennsylvanian (Middle Virgilian) Hartford Limestone of Hamilton Quarry, Kansas. The new genus

is related to "typical" Mesozoic hybodontoids such as *Hybodus* and *Acroodus*. *Hamiltonichthys* is the first articulated hybodontoid to be described from North America, and is the oldest complete hybodontoid known thus far.

INTRODUCTION

Hybodus and its allies (e.g., *Acroodus*, *Asteracanthus*) were common elasmobranchs during most of the Mesozoic era, and apparently occupied a wide range of aquatic habitats. Despite the paucity of well-preserved fossil specimens, it is now known that the cranial anatomy of these hybodontoid sharks was specialized (Maisey, 1982, 1983). Morphological peculiarities of the neurocranium, mandibular suspensorium, and dermal skeleton suggest that these hybodontoids collectively form a monophyletic group (Maisey, 1987). The previously popular notion that some or all Recent elasmobranchs are de-

scended from a *Hybodus*-like ancestor does not withstand critical investigation and cannot be substantiated on anatomical grounds (Maisey, 1982), although it is still maintained in some noncladistic studies (e.g., Thies, 1983; Thies and Reif, 1985; Reif, 1985). Supposedly "transitional" fossils (e.g., *Palaeospinax*, *Synechodus*) certainly share some apomorphic skeletal characters with Recent elasmobranchs, but possess none of the derived attributes of Mesozoic hybodontoids (Maisey, 1977, 1984a, 1984b, 1985). Recent Heterodontidae (Port Jackson sharks) and Mesozoic hybodontoids share only plesio-

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Fig. 1. *Hamiltonichthys mapesi*, g. and sp. nov., holotype; A, part, KUVP 86308; B, counterpart, AMNH 10807. Entire female individual, UV fluorescent image.

morphic characters (e.g., the presence of dorsal fin-spines and a large basal plate in the anal fin) and convergent characters (e.g., low-crowned teeth, heterodonty, and jaws with a strong ethmoidal support). A close relationship between these hybodontoids and *Heterodontus* is no longer feasible (Maisey, 1982), although some other fossils previously regarded as "hybodonts" (e.g., *Synechodus*, *Orthacodus*) may have affinity with Recent galeomorphs or *Heterodontus* (Maisey, 1985; Cappetta, 1987).

The cranial anatomy is now known in some Mesozoic hybodontoids, including *Hybodus reticulatus* (considered to be the type species of *Hybodus*; Koken, 1907; Woodward, 1916; Maisey, 1987). The postcranial skeleton is known in a few cases, where it is anatomically conservative (Maisey, 1982). One of the most striking peculiarities is the presence of elongate pleural ribs, although the systematic value of this feature is unsettled (Dick, 1978; Dick and Maisey, 1980; Maisey, 1982). Hybodontoids primitively possess paired cephalic spines and distinctive fin-spine morphology (Maisey, 1978, 1982). Various morphological and histological criteria of the teeth have been used in phylogenetic studies of hybodontoids, but the systematic value of such data has proven highly controversial (Glikman, 1964, 1967; Patterson, 1966; Reif, 1973, 1978a; Maisey, 1982, 1987). Dermal denticles have also been investigated (e.g., Reif, 1978b) but their value in systematic studies seems limited (Reif, 1985).

During the 19th and early 20th centuries it was customary to regard a great many isolated Upper Paleozoic chondrichthyan teeth, fin-spines, and other dermal structures as evidence of early "hybodonts," without much regard to the possibility of greater taxic diversity. Determining the systematic position and status of most taxa founded upon such disparate fragments is problematical, but with the discovery of articulated Late Paleozoic chondrichthyans at Bear Gulch (Montana), Bearsden (Scotland), and elsewhere, it is finally becoming evident that chondrichthyans underwent profound taxic diversification early in their evolutionary history and that many lineages developed bizarre and spe-

cialized dermal defenses. Although this early radiation is poorly resolved, two of the putative lineages involved are of particular interest here. One of these includes sharks possessing teeth, cephalic spines, and fin-spines like those of the Mesozoic Hybodontoidae (Hay, 1899; Hussakof, 1911; Woodward, 1934; Romer, 1942; Zidek, 1969; Lund, 1970; Berman, 1970; Bendix-Almgreen, 1975; Johnson, 1981; Maisey, 1982), while the other includes form-taxa (presently known only from fragmentary dermal remains) with tooth, denticle, and fin-spine morphologies resembling those of Recent elasmobranchs (Reif, 1977; Reif and Goto, 1979; Duffin, 1980, 1982a, 1982b; Maisey, 1982, 1984b; Thies, 1983; Duffin and Ward, 1983; Turner, 1982, 1985).

Historically, a large number of other Paleozoic form-taxa have also been considered "hybodonts." Space precludes further discussion here, but these assignments are generally ill-founded (see Maisey, 1982, for a review). Until recently, *Tristychius* and *Onychoselache* were the only articulated Paleozoic elasmobranchs which seemed even remotely related to Mesozoic hybodontoids (Dick, 1978; Dick and Maisey, 1980).

An abandoned quarry in an Upper Pennsylvanian sequence near Hamilton, eastern Kansas, has yielded a small sample of well-preserved hybodontoid elasmobranchs. These specimens provide an insight into the earlier history of "hybodont" sharks, and may eventually help to place the enigmatic taxa *Tristychius* and *Onychoselache* within a less chaotic phylogenetic perspective. To some extent, the Hamilton "hybodonts" also contribute to a better understanding of the putative relationship between Recent elasmobranchs and the hybodontoids. This new material represents the first articulated hybodontoid to be documented from North America, as well as the oldest articulated hybodontoid so far recorded.

MATERIALS AND METHODS

The Hamilton hybodont is described here on the basis of eight specimens (see below, systematic section). Six of these represent

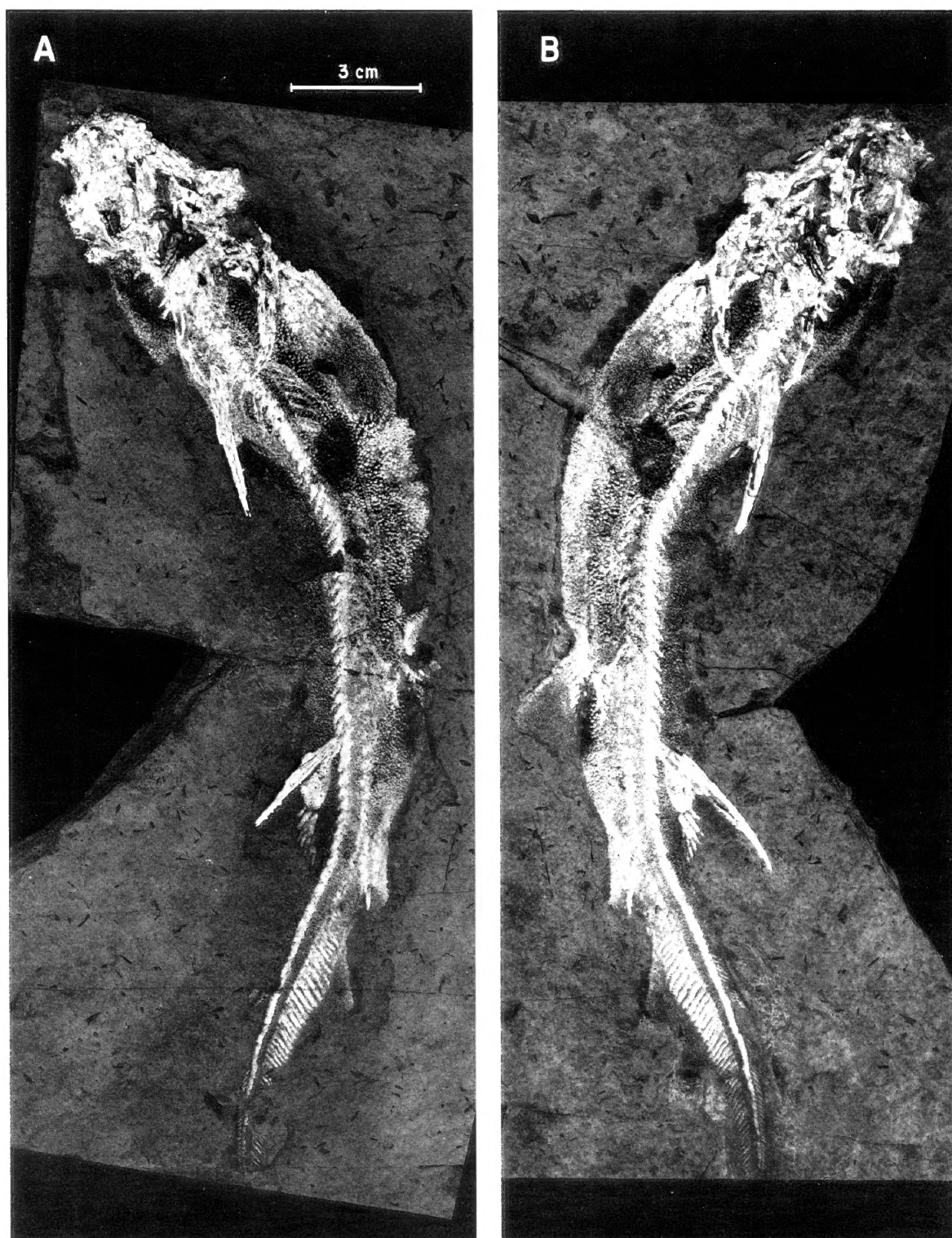


Fig. 2. *Hamiltonichthys mapei*, KUVF 65016, part (A) and counterpart (B) of complete female individual. UV fluorescent image.

complete individuals. The most complete is designated the holotype of a new genus and species. The other two specimens are fragmentary; one is a caudal fin and the other consists of four associated lateral teeth within a coprolite. All the specimens are preserved in a thin-bedded argillaceous limestone containing a moderate amount of organic debris, especially carbonized plant fragments. The bedding planes on which the fishes are preserved are uneven, although it remains to be determined whether this is a result of diagenesis or of postdiagenetic disturbance. The specimens described here are all compressed, but are otherwise well preserved. The calcified endoskeleton and dermal skeleton are particularly clear, and the squamation gives us a good idea of body shape, fin position, and size. So much is preserved that interpretation becomes difficult where structures have become crushed on top of one another, for example in the pharyngeal region.

In spite of the excellent state of preservation, much of the finer detail only becomes apparent using various fairly sophisticated techniques. Virtually every photograph in this work was taken with ultraviolet fluorescence or reflected-UV microphotography, a scanning electron microscope, or x-ray photography. Thus many of the features illustrated would be poorly visible, or even invisible, if conventional microscopical techniques had been used. This point is stressed in order to encourage other investigators of the important Hamilton Quarry biota to explore as broad a range of preparatory and illustrative techniques as possible. A brief note of the various methods employed is given here.

The specimens required little mechanical preparation, and we chose not to make acid preparations by the transfer method. Some denticles were removed using dilute acetic acid. Where it was found necessary to clean small areas of matrix (e.g., around some teeth), excellent results were obtained by first immersing the fossil in Waller's Solution (for technique, see Waller, 1980; King, 1983), which contains sodium citrate (to sequester ferrous ions), sodium dithionite (a reducing agent), and sodium bicarbonate (to maintain neutrality). This immersion reduces ferrous ions in the matrix, rendering them water-sol-

uble. The limestone matrix becomes slightly softer and hence more amenable to preparation using mounted needles. Teeth were cleaned from the matrix better using this technique than by using acid.

Detailed investigation and microphotography of the specimens were mainly conducted under long-wave (3660 Å) ultraviolet light (for details, see Rolfe, 1965). The skeletal material fluoresces a pale lemon yellow (calcified cartilage) or deep yellow to orange (teeth, fin-spines, squamation). Small areas were illuminated by mercury-vapor spot sources, but for views of entire specimens (e.g., figs. 1–5) it was necessary to cluster several small 15W blacklight tubes over the whole area. Exposures varied in duration up to approx. 20 minutes, depending on relief, degree of fluorescence, and aperture setting.

Scanning electron microscopy of teeth and scales was conducted using a Cambridge Stereoscan-250 system operating at 10 kV. Specimens were gold sputter-coated. Denticles and a broken tooth were examined after being freed from the matrix by the Waller technique (see above). Sections of the dentitions of two specimens were also investigated by SEM, by making high-density epoxy casts from "Silastic" molds, and using the casts in place of the actual specimens (which were too large for the vacuum chamber). As the published figures show, there is no appreciable loss of detail at the levels of magnification used, and this technique provides views at otherwise unobtainable orientations.

Reflected-fluorescence microphotography of epoxy tooth casts (sometimes in conjunction with visible light) was also utilized. By taking advantage of the shorter reflected wavelengths, this technique virtually doubles the resolution of fine detail in small objects.

In general, the limestone matrix did not provide clear x-ray images, probably because ferruginous matter within the limestone, as well as the calcium itself, was blocking some of the radiation. Some details of the pharyngeal region were revealed in KUVF 86307, in which the matrix is extremely thin (fig. 7).

Comparisons are made throughout the text with many Recent and fossil elasmobranchs. It was originally intended to illustrate many



Fig. 3. *Hamiltonichthys mapesi*, KUVP 65017A, complete male individual with plant frond obscuring part of head. UV fluorescent image.



Fig. 4. *Hamiltonichthys mapesi*, KUVP 86304, complete female individual. UV fluorescent image.

of the comparative features by means of line drawings and/or photographs, but these plans were abandoned in order to publish the descriptive account in a timely manner. It is hoped that sufficient references are given in the text to enable the interested reader to seek out pertinent literature.

ON THE NAMING OF ICHTHYOLITHS

Following the formal systematic diagnosis below, I have appended a second ichthyolith diagnosis, utilizing the terminology and enumeration recently developed by Tway and Zidek (1982, 1983a, 1983b) for describing isolated microscopic fish skeletal remains from the Late Pennsylvanian of North America. My purpose in doing this is not to assign particular taxonomic handles to their un-named categories. Indeed, to do so would in my opinion be a retrograde step to the dark ages of paleontological investigation, when every ichthyolith scrap was assigned a binomial albatross to wear around its neck. Jaekel (1889) long ago discovered that the proliferation of genera and species founded upon scraps of fossil vertebrates can create enormous nomenclatural problems. Even where certain categories of ichthyolith remains can be shown to occur in a fossil species, it would be foolhardy indeed to attempt to synonymize all such similar ichthyoliths, given the taxonomically unstructured descriptor system devised by Tway and Zidek (1982, 1983a, 1983b).

Although their system certainly avoids the pitfalls of traditional nomenclatural practice, it can nevertheless be criticized for its lack of internal cohesiveness. Teeth and denticles that may be parts of morphological transformation series have different descriptors. Furthermore, it is obvious from the present investigation that a broad range of profoundly different ichthyoliths can pertain to a single fossil species, and that more than one descriptor (e.g., 018, 202) may be applicable to the same dermal elements.

It may ultimately be possible to develop a comprehensive multielement taxonomic system for vertebrate ichthyoliths that approaches the one developed by conodont workers in stratigraphic and biological utility.

Progress in this direction has already been made by Hansen (1986), who has analyzed microscopic chondrichthyan remains from 106 localities in marine Pennsylvanian sequences of Ohio and adjacent regions.

Drawing upon the multielement approach utilized by conodont investigators, Hansen (1986) recognized 34 chondrichthyan species, 18 of which are founded on teeth and 16 on denticles. A degree of taxonomic redundancy is doubtless inherent in his procedure, since some of the species founded on different elements (teeth, scales) are probably synonymous. Hansen's (1986) methodology, being based on multielement analysis, nevertheless offers a considerable taxonomic and biostratigraphic advantage over the earlier nomenclatural practice of naming every scrap, as well as over the relatively unstructured practice of assigning a descriptor code.

In giving an ichthyolith diagnosis, it is simply my intention to indicate which categories of ichthyolith have been identified in the material under investigation. It is readily apparent from my diagnosis that a broad range of ichthyolith morphologies occur in this species.

If future investigations of other articulated fossil remains follow the present example, it may be possible to generate a multielement ichthyolith data base for many fossil chondrichthyan species. Such a data base would undoubtedly be informative to stratigraphers, paleoecologists, and systematists, and would permit even closer collaboration among their disciplines.

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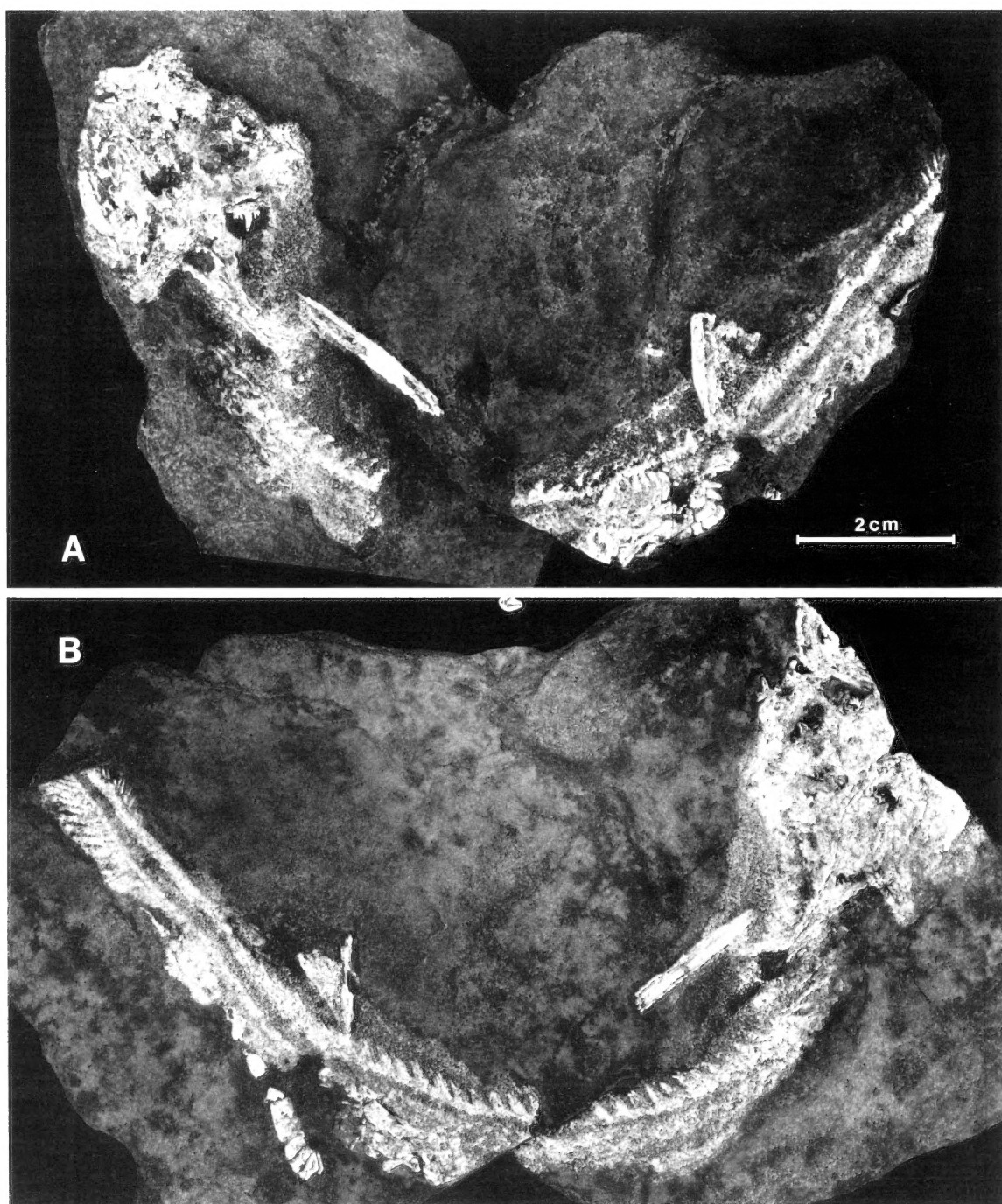


Fig. 5. *Hamiltonichthys mapesi*, KUPV 86305, part (A) and counterpart (B), male individual lacking part of head and caudal extremity. UV fluorescent images.

logical Sciences, Ohio University, Athens), who collected some of the specimens and in whose honor the species is named. My investigation has benefited from valuable dis-

cussions with Drs. R. Lund (Adelphi College, N.Y.), R. Zangerl (Field Museum of Natural History, Chicago), B. Schaeffer, and the late D. Rosen (American Museum of Natural

History). Dr. M. Hansen (Ohio Geological Survey) has provided valuable criticism of the manuscript, and has patiently explained the relative merits of multielement, descriptor, and "traditional" analysis of vertebrate ichthyoliths to me. Dr. B. Stahl (St. Anselm College, Manchester, N.H.) also reviewed the manuscript and offered many helpful improvements, all of which were incorporated. I thank O. Rieppel (University of Zürich) for giving me access to *Acronemus*, *Palaeobates*, and *Asteracanthus* material, and K. S. Thomson (then at Yale Peabody Museum; now at Philadelphia Academy of Sciences) for access to the Madagascar "*Acrodus*." This research was supported in part by the National Science Foundation (award no. BSR83-08419). The complex illustrations were prepared by Ms. Lorraine Meeker and Mr. Chester Tarka. Versions of the manuscript were typed by Ms. Alejandra Lora and Cathy Szymanski, and the submitted version was edited by Ms. Brenda Jones.

ABBREVIATIONS

Institutional

AMNH American Museum of Natural History
KUPV Kansas University, Vertebrate Paleontology Collection

Anatomical

b basal
bbr basibranchial
bh basihyal
bpt basipterygium
cbr ceratobranchial
ch ceratohyal
cik caudal internasal keel
cor coracoid part of scapulocoracoid
df diazonal foramen
end f endolymphatic fossa
f hyp hypophyseal fenestra
gf glenoid fossa
hbr hypobranchial
hym hyomandibula
i intermediate cartilage
jc jugular canal
Mc Meckel's cartilage
mes mesopterygium
met metapterygium
mpt mixipterygium
oc cot occipital cotylus
ot cap otic capsule
pdbc posterior dorsal basal cartilage
pdsp posterior dorsal fin-spine
pnw postnasal wall

popr postorbital process
pq palatoquadrate
prcf precerebral fontanelle
pro propterygium
r radial
scap scapular part of scapulocoracoid
subs suborbital shelf
supcr supraorbital crest

GEOLOGIC OCCURRENCE

The history of collecting at Hamilton Quarry is briefly reviewed by Zidek (1976), who recorded a varied vertebrate fauna including a dissorophid amphibian, a lungfish, paleoniscoid fishes, numerous *Acanthodes* (particularly immature specimens), a xenacanth shark, and the hybodonts. Also collected at Hamilton were eurypterids (Andersen, 1974), arachnids, insects (Hanson, 1973), myriapods, ostracods, and an abundant flora, said by Zidek (1976) to bear a close resemblance to that known from Garnett, Kans.

The age of the Hamilton flora and fauna is not yet firmly established, although the Pre-Atokan (Lower Pennsylvanian) date postulated by Andersen (1974) now seems too old. Rocks of Morrowan age (Lower Pennsylvanian) are thought to be restricted to the Hugoton Embayment (western Kansas). The succeeding Atokan stage is mainly restricted to the south-west, although some Atokan shales occur beneath the Demoinesian in parts of eastern Kansas (Ebanks et al., 1979). Zidek (1976) reported previously unpublished findings by Professor Thomas E. Bridge (Emporia State College), placing the beds either within the Hartford Limestone Member of the Topeka Limestone Formation (i.e., uppermost Shawnee Group) or else as a post-Topekan (i.e., Wabaunsee Group) erosional channel deposit within the Hartford Limestone and the underlying Calhoun Shale formations. In either case, Bridge asserted that the fossiliferous clastic limestones of Hamilton Quarry are of Middle Virgilian age, and represent infilling of an erosional channel. Zidek (1976) further suggested that the depositional environment was a very low-energy regime, allowing the preservation of extremely delicate plants, invertebrates, and juvenile acanthodian fishes. This scenario for the age and paleoenvironment of the Hamilton biota is provisionally accepted with one reservation:



Fig. 6. *Hamiltonichthys mapesi*, KUV 86307, anterior part of individual, sex not determined, showing basicranium and palatoquadrate. UV fluorescent image.

according to Bridge there ought to be a post-Topekan erosional surface with which the channel would be associated, but Ebanks et al. (1979) stated that the Wabaunsee Group "conformably overlies the Shawnee Group and caps the Virgilian Stage and Pennsylvanian System in Kansas." Besides the dis-

crepancy over conformity between the Wabaunsee and Shawnee groups, Ebanks et al. (1979) leave some doubt as to whether the Wabaunsee Group is itself Pennsylvanian or Permian in age. According to them the Wabaunsee Group is conformably overlain by Lower Permian rocks.

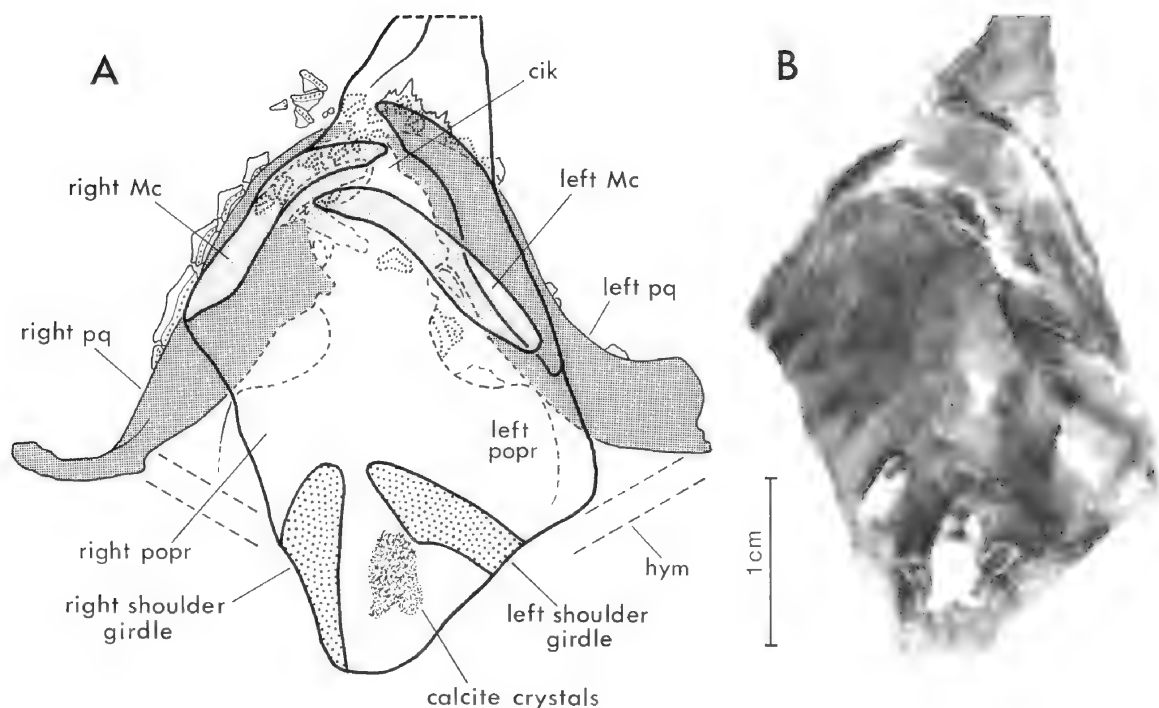


Fig. 7. Principal features of head in KUVp 86307; **A**, outline of salient morphology, rendered from part (fig. 6) and counterpart; **B**, the counterpart (positive print from x-ray). Note that views in figures 6 and 7 are to the same scale and have the same orientation to facilitate comparison.

SYSTEMATICS

CHONDRICHTHYES

ELASMOBRANCHII

PLESION HYBODONTIFORMES

SUBORDER HYBODONTOIDEI

Hamiltonichthys, g. nov.

DIAGNOSIS: Hybodontoid sharks of approximately 300 mm total length, with low-crowned teeth, each with a single asymmetrical peak; teeth traversed by numerous cristae, with a lingual swelling and continuous shoulder; lower dentition comprising a symphyseal series, six anterior lateral series, a single elongate lateral series, and a single short posterior series; upper dentition comprising parasymphyseal series, six anterior lateral series, single long lateral series, and single short posterior series; jaws broad, lacking postorbital articulation; four simple multicuspid cephalic spines in males, each cusp with an open pulp cavity; pharyngeal dentition consisting of several multicuspid tooth-whorls; pelvic girdle a continuous pubois-

chiadic bar only in males; posterior dorsal fin with metapterygial-like axis; anal fin supported by series of small cartilage plates.

ETYMOLOGY: After the type locality.

TYPE SPECIES: *Hamiltonichthys mapesi*, g. nov., sp. nov.

Hamiltonichthys mapesi, g. nov., sp. nov.

DIAGNOSIS: As for genus.

ETYMOLOGY: In recognition of Dr. Royal Mapes, whose collecting at Hamilton Quarry has done much to further the interests of paleontology, including the discovery of the specimen designated here as the holotype.

HOLOTYPE: KUVp 86308 (part) and AMNH 10807 (counterpart); female (fig. 1).

Other Referred Material:

KUVp 86304 (formerly HQ 106); female (fig. 4).
KUVp 86305 A & B (formerly HQ 266, 268); male (fig. 5).

KUVp 86307 A & B (formerly HQ 270), sex indeterminate (figs. 6, 7).

KUVp 65016 A & B; female (fig. 2).

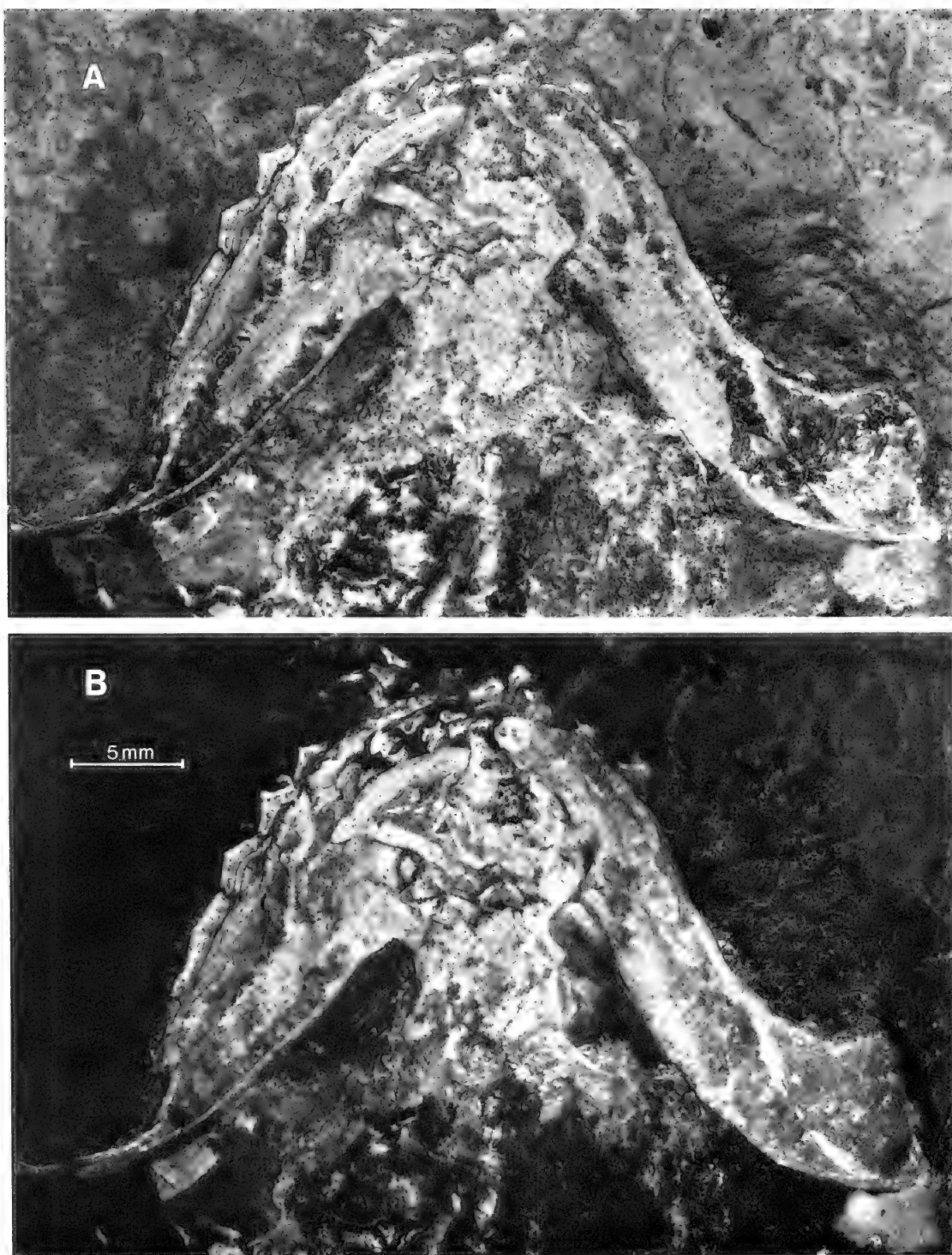


Fig. 8. *Hamiltonichthys mapesi*, KUVP 86307. Enlarged views of head, both to same scale; **A**, white light (tungsten) illumination; **B**, UV fluorescent image. Different aspects of the morphology can be seen by varying the source of illumination. Note well-developed ethmoidal articulation. Specimen has split open obliquely, so that the ethmoidal region is exposed in ventral view, but the neurocranial walls are split through behind the orbits, and the otico-occipital region is essentially an internal mold of the dorsal surface.

KUVP 65017 A & B; male (fig. 3).
KUVP 88641; sex indeterminate (not figured: caudal fin only).
KUVP 87870; four lateral teeth in coprolite (not figured).

Unit Horizon and Locality: Upper Pennsylvanian, Middle Virgilian, Upper Shawnee Group or Wabaunsee Group, Hartford Limestone, Hamilton Quarry, Sec. 8, T24S, R12E, Greenwood County, Kansas.

Ichthyolithic Diagnosis (after Tway and Zidek, 1982, 1983a, 1983b): See table 1.

COMMENTARY

In the following description of *Hamiltonichthys*, I compare *H. mapesti* with several species of Mesozoic Hybodontoides and various Paleozoic elasmobranchs, particularly *Tristychius* and *Onychoselache*. In the case of these two genera, my taxonomic usage follows that of Dick (1978; see also Dick and Maisey, 1980), which is rather different from that of earlier investigators (e.g., Traquair, 1888; Woodward, 1924; Moy-Thomas, 1936), whose "*Tristychius arcuatus*" is the equivalent of *Onychoselache traquairi* Dick. Among the Hybodontoides, many nominal species (mostly founded upon isolated teeth and fin-spines) have been assigned to a few genera (e.g., *Hybodus*, *Acroodus*, *Polyacrodus*, *Asteracanthus*, *Lonchidion*). Some progress is being made toward assigning certain species to new genera (e.g., *Egertonodus*, containing *Hybodus basanus* and *H. fraasi*; Maisey, 1987). Other taxa have been removed altogether from the Hybodontoides, and have been shown to be related to Recent elasmobranchs (e.g., *Palaeospinax*, *Synechodus*; Maisey, 1977, 1982, 1985).

I have been able to examine the two articulated specimens of "*Hybodus*" *cassangensis* from the Triassic of Angola described by Teixeira (1954, 1956, 1978; see also Maisey, 1982). From the impressions of teeth preserved in one of these specimens, I tentatively assign this species to *Lissodus* pending a revised description, and it is referred to below as *L. cassangensis*.

DESCRIPTION

BRAINCASE. No single specimen of *Hamiltonichthys mapesti* has a complete braincase. A composite partial reconstruction of the neurocranium is shown in figure 10.

The cranium is broadest at the postorbital processes, between which are located the otic capsules and a small, ovoid endolymphatic (parietal) fossa. Anteriorly there is a broad precerebral fontanelle. There is no indication of basal communicating canals. On its ventral side, the ethmoid region forms a median internasal keel (fig. 7), with which the palatoquadrates are articulated just anterior to the point at which the keel broadens into the suborbital shelf. It has not been determined by direct observation whether *Hamiltonichthys* possessed a paired ethmopalatine process as in *Egertonodus basanus*. The postnasal wall was well developed, but it is uncertain whether an ectethmoid process was present. The olfactory region is broader than in *Egertonodus*, but less so than in many Recent elasmobranchs (e.g., *Heterodontus*).

In the orbitotemporal region the supraorbital shelves are well developed. The interorbital wall cannot be studied in the available material, and the positions of various cranial

Table 1

Section no.	Subtype no.	Colloquial name	Structure/ position
I	062	Three peaks, three keels	Denticle/trunk, fins
I	089	Three peaks, cruciform platform	Denticle/trunk, fins
I	199	Three peaks, subcircular platform	Denticle/trunk, fins
I	224	Three peaks, triangular platform	Denticle/trunk, fins
I	229	Three peaks, lobed platform	Denticle/trunk, fins
VIII	018	Many cusps striated & curved	Tooth whorl/pharynx
VIII	202	Round curved cusps	Tooth whorl/pharynx
X	140	Flat surface radiating lines	Denticle/snout

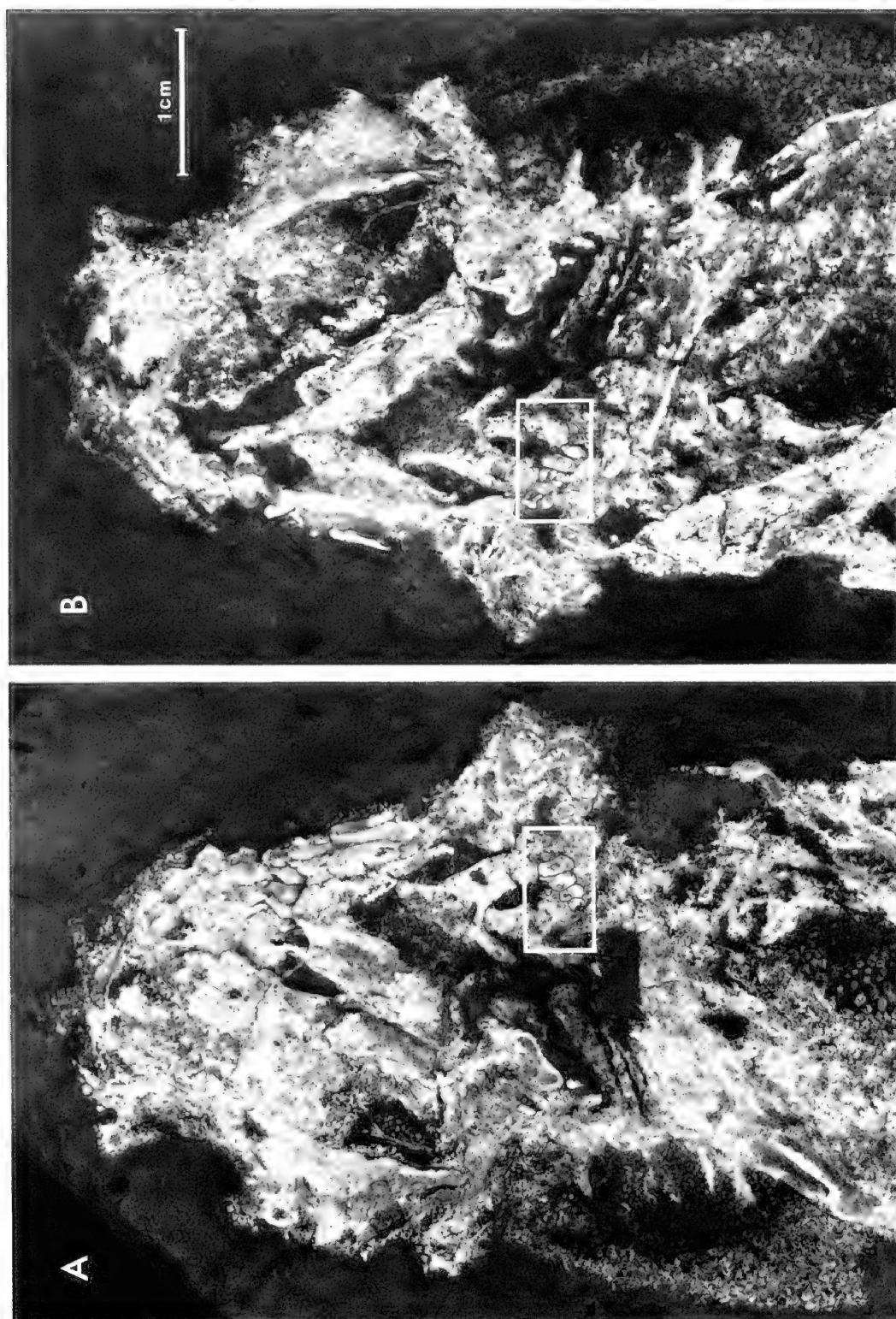


Fig. 9. *Hamiltonichthys mapesi*, KUVF 65016, details of head, part (A) and counterpart (B) to same scale. Boxed areas indicate location of pharyngeal tooth-whorls. UV fluorescent image.

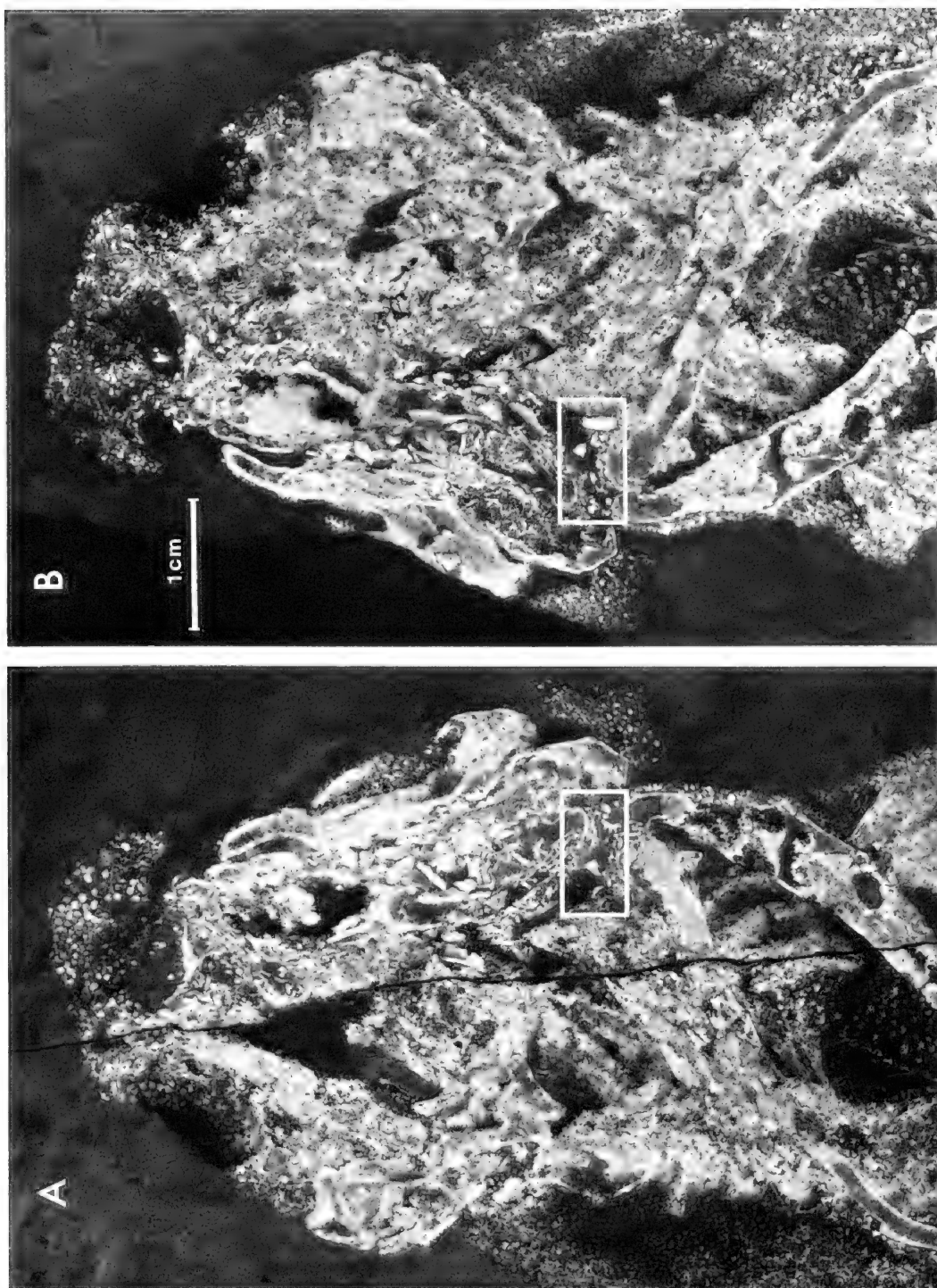


Fig. 10. *Hamiltonichthys mapesi*, holotype, details of head. **A**, part (KUPV 86308); **B**, counterpart (AMNH 10802) to same scale. UV fluorescent image. Boxed areas contain pharyngeal tooth-whorls (discussed in text).

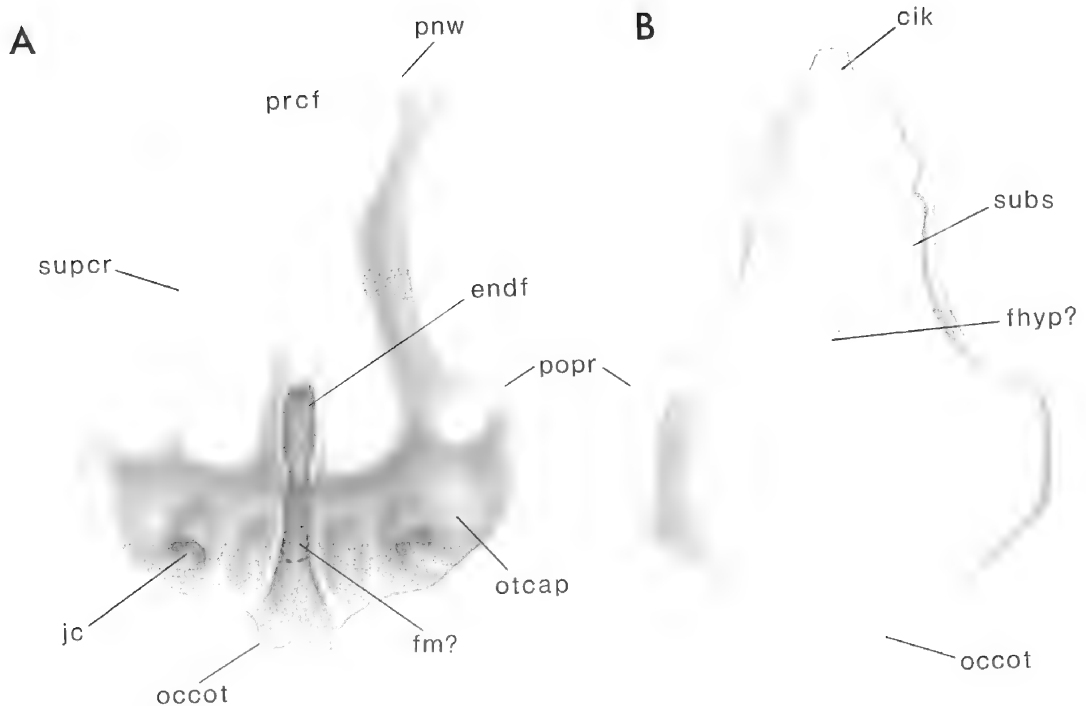


Fig. 11. Reconstruction of neurocranium in *H. mapesi*. **A**, dorsal view, with otic region between postorbital processes; **B**, ventral view showing folds in anterior part of suborbital shelf, forming ethmoidal articulation. Pencil rendering.

foramina have not been determined. The cranial roof between the endolymphatic fossa and the precerebral fontanelle is completely covered by prismatic calcified tissue (fig. 9). In Recent elasmobranchs this region (formed in part by the tectum antoticum; de Beer, 1931, 1937) is one of the last to chondrify; its chondrification occurs particularly late in orectoloboids, and the braincase roof may remain partially open (forming the "posterior fontanelle") in adult batoids (Holmgren, 1940, 1941).

The basicranium of KUV P 86307 is also fully chondrified (fig. 8). A median pitlike area may represent the internal carotid foramen and/or hypophyseal fossa (hyp?; fig. 10). If this interpretation is correct, the pit denotes the approximate level of fusion between parachordal and trabecular moieties of the developing braincase. These regions were apparently of subequal length in *Hamiltonichthys*, as in *Egertonodus basanus* and *Hybodus reticulatus* (Maisey, 1983, 1987).

In *Hamiltonichthys* the occiput, otic capsules, and postorbital process are arranged as in *Egertonodus basanus*. The occipital arch

extends anteriorly between the posterior parts of the otic capsules, which are located mesial to the postorbital processes (fig. 10). The occiput also extends behind the otic capsules, as in *Egertonodus basanus* and many Paleozoic elasmobranchs. The lateral otic process has not been located in *Hamiltonichthys*, but its probable position (suggested in KUV P 65016 and 86307) is anterolateral to large paired openings. The latter may represent either the posterior end of the jugular canal, or else the vagus-glossopharyngeal fossa (suggested by comparison with *Egertonodus basanus*).

Although the glossopharyngeal canal has not been located with certainty in *Hamiltonichthys*, the absence of basicranial foramina in the otic region suggests that the hypotic lamina was well developed. By contrast, where the hypotic lamina is absent (e.g., in holocephalans), the glossopharyngeal and vagus nerves emerge ventrally.

VISCERAL SKELETON. The jaws are exposed to KUV P 86307, 65016, and 65017 (figs. 3, 6, 8, 11). In 86307 and 65016, the head is flattened dorsoventrally, and the pal-

atoquadrate are splayed out from their ethmopalatine articulation with the braincase (fig. 7A). In KUV 65017 the braincase is again exposed in ventral aspect, but the jaws are displaced and the lateral surfaces of the right palatoquadrate and mandible are seen (fig. 3).

The broad mandibular arcade is sigmoidally curved, with the mandibular joint located lateral to the otic capsules. There is a well-developed articular surface on the anteromesial surface of the palatine ramus of the palatoquadrate (figs. 7, 8), in approximately the same position as the ethmoidal articulation in *Hybodus*, *Egertonodus*, *Xenacanthus*, and *Synechodus* (Hotton, 1952; Maisey, 1982, 1983, 1985). In *Hybodus* and *Egertonodus*, however, there is an additional articular surface anterodorsally. The palatoquadrate is sandwiched between the suborbital shelf and an ethmopalatine process. *Hamiltonichthys* appears to lack the more dorsal palatoquadrate articulation. Its presence is regarded here as a derived character within hybodontoids.

Anterior to the ethmoidal articulation, the palatine ramus curves beneath the orbitonasal lamina toward its antimer. The palatoquadrate apparently did not have a cartilaginous symphysis, and were probably separated by the ethmoidal internasal keel, as in *Hybodus*, *Egertonodus*, and *Xenacanthus* (the "rostral articulation" of Schaeffer, 1981: 56). The teeth lie within a distinct but shallow dental groove, extending from the symphyseal area to a point approximately three-quarters of the length along the palatoquadrate. The adductor fossa begins just behind this point. The mandibular joint has a double arrangement, as in elasmobranchs generally, but is otherwise unremarkable. There is no evidence of a postorbital articulation.

The quadrate moiety of the upper jaw is curved away from the braincase, and there cannot have been a sliding contact with the floor of the otic region as occurs in *Egertonodus* and *Hybodus* (Maisey, 1982, 1983, 1987).

A hyomandibula has been identified in KUV 86307, passing from the mandibular joint toward the posterior end of the otic region (figs. 6, 7A). This orientation of the hyomandibula in *Hamiltonichthys* is probably

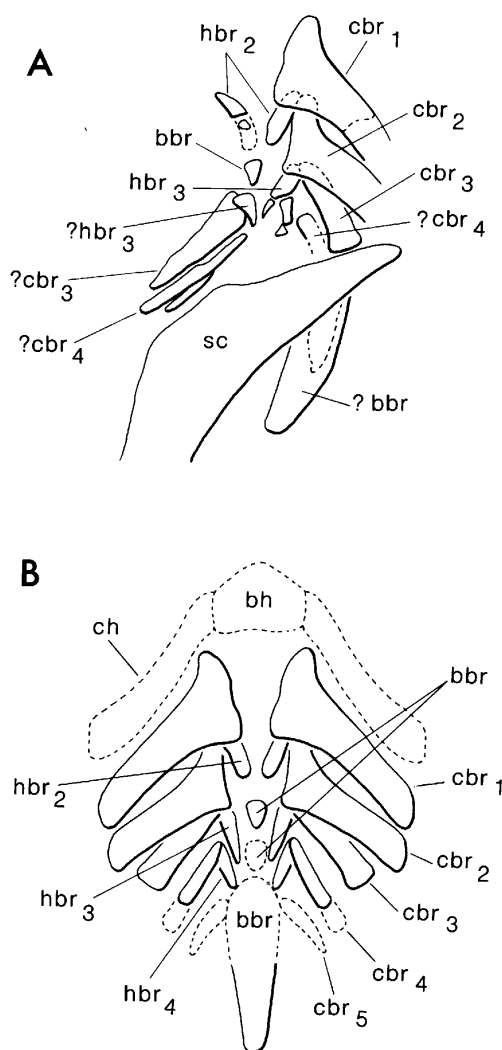


Fig. 12. Outline rendering (A) and reconstruction (B) of the ventral branchial skeleton in *H. mapei*, based on KUV 65016.

related to the relatively shortened gape as in some Recent elasmobranchs (e.g., *Squalus*, oreotoloboids, *Heterodontus*), and is different from that described in *Hybodus* and *Egertonodus* (Maisey, 1982, 1983). The ceratohyal has not been positively identified, although parts of it may be present in the counterpart of KUV 86307 (seen in x-ray; fig. 7B).

Some parts of the branchial skeleton are preserved in KUV 65016 and the holotype. As far as can be determined, five branchial arches are present, with characteristic elasmobranch architecture, as in *Lissodus casangensis* and *Egertonodus fraasi* (Maisey,

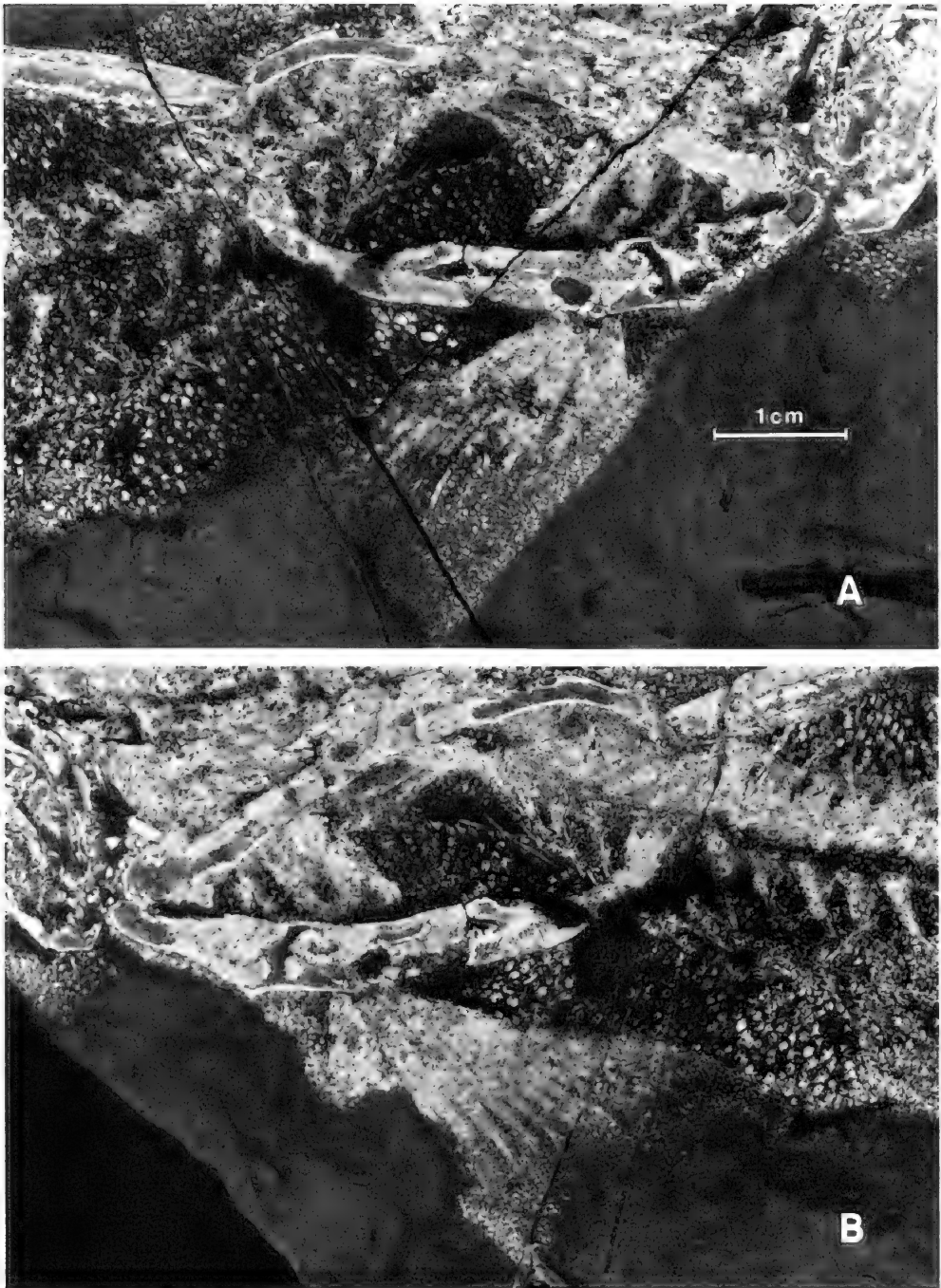


Fig. 13. *Hamiltonichthys mapesi*, holotype, pectoral girdle and fins; A, KUV 86308; B, AMNH 10807. UV fluorescent image (see fig. 14 for explanation).

1982: fig. 9A, B, D). Parts of the branchial skeleton are also faintly discernible in x-rays of the counterpart of KUV 83607 (fig. 7B). In KUV 65016, an *en echelon* series of paired elements is present (fig. 11). Smaller paired

central elements are flanked by larger overlapping ones. From the overlap, shape, and position of these larger elements, I conclude that they are ceratobranchials, and that the smaller series represent hypobranchials. Be-

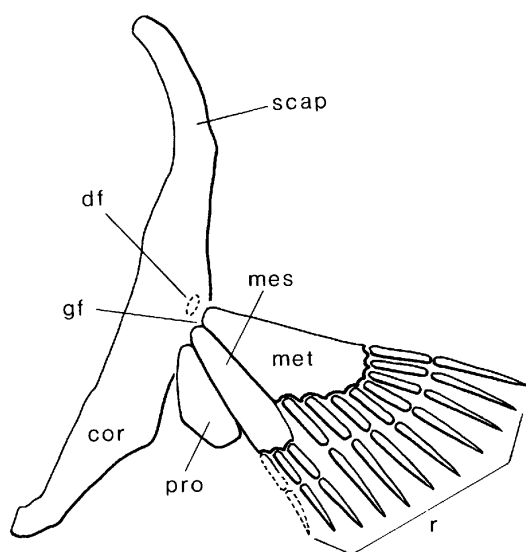


Fig. 14. Outline reconstruction of scapulocoracoid and pectoral fin skeleton in *H. mapesi*, based mainly on the holotype (see fig. 13).

hind one of the endoskeletal shoulder girdles is an elongated, posteriorly directed cartilage which may be the basibranchial copula. An outline restoration of the ventral gill-arch morphology is given in figure 12.

AXIAL SKELETON. Six specimens of *Hamiltonichthys* are almost complete apart from their caudal extremities, and the number and arrangement of elements in the axial skeleton can be fairly accurately determined (figs. 1–5).

There are no calcified vertebral centra, and the axial skeleton consists for the most part of neural and hemal elements, as in *Hybodus* (Maisey, 1982: fig. 10). In the vicinity of the branchial arches the precise number and arrangement of neural arches are uncertain, but there were probably about 10 between the occiput and base of the first dorsal fin-spine. There are between 30 and 32 neural arches between the first and second fin-spines, followed by 16 as far as the first epichordal radials of the caudal fin. Within the tail there are at least 50 additional dorsal elements, but the tip of the tail is generally missing and the actual number of caudal elements may have been more like 55 or 60.

Each neural element has a corresponding ventral component. Anteriorly there is a ribcage comprising 13 or 14 elongate pairs of ribs, of which the sixth is the longest. The

ribs become progressively shorter again posteriorly, and merge with the series of hemal arches below the first dorsal fin. From here to the anal fin the hemal elements become shorter and squatter, but they rapidly lengthen again at the base of the caudal fin, reaching a maximum length opposite the start of the epichordal radials.

Spinal nerve foramina have not been located in the dorsal arcualia of *Hamiltonichthys*. These elements are nevertheless arranged one-to-one with the ribs, suggesting homology with Recent gnathostome interdorsals which occupy a primary (neural) position. This was also postulated for Mesozoic hybodontoid dorsal arcualia, using the same topographic criteria (Maisey, 1982: fig. 11).

FINS. The size and shape of the various fins can be determined from the extent of their squamation. No traces of ceratotrichia now remain. Toward the fin margins, however, dermal denticles are arranged in rows parallel to where the underlying ceratotrichia would be expected. The fin endoskeletons are generally calcified and well preserved.

PAIRED FINS: The pectoral fins are nearly triangular, but their leading edge is somewhat convex (figs. 13, 15). The attachment area to the scapulocoracoid is narrow, and the glenoid fossa is correspondingly small (fig. 14). Separate suprascapulars have not been found. In comparison with Mesozoic Hybontoidei, the scapulocoracoid of *Hamiltonichthys* is slender. The coracoid region is only one-third as long as the scapular moiety, whereas in Mesozoic Hybontoidei the two regions are of almost equal length. In the type specimen of *H. mapesi* there is evidence of at least one and perhaps two openings for the diazonal innervation of the pectoral fins, adjacent to the glenoid fossa (fig. 13).

The pectoral fin of *H. mapesi* is tribasal. As in *Lissodus cassangensis*, *Hybodus hauffianus*, and most Recent elasmobranchs, articulation with the scapulocoracoid is mainly propterygial, although the mesopterygium and metapterygium may also have met the shoulder girdle (Maisey, 1982: fig. 12). Such an arrangement suggests a high degree of rotational mobility for the pectoral fin.

The propterygium of *Hamiltonichthys* apparently lacks calcified radials. The mesopterygium carries at most three radial series,

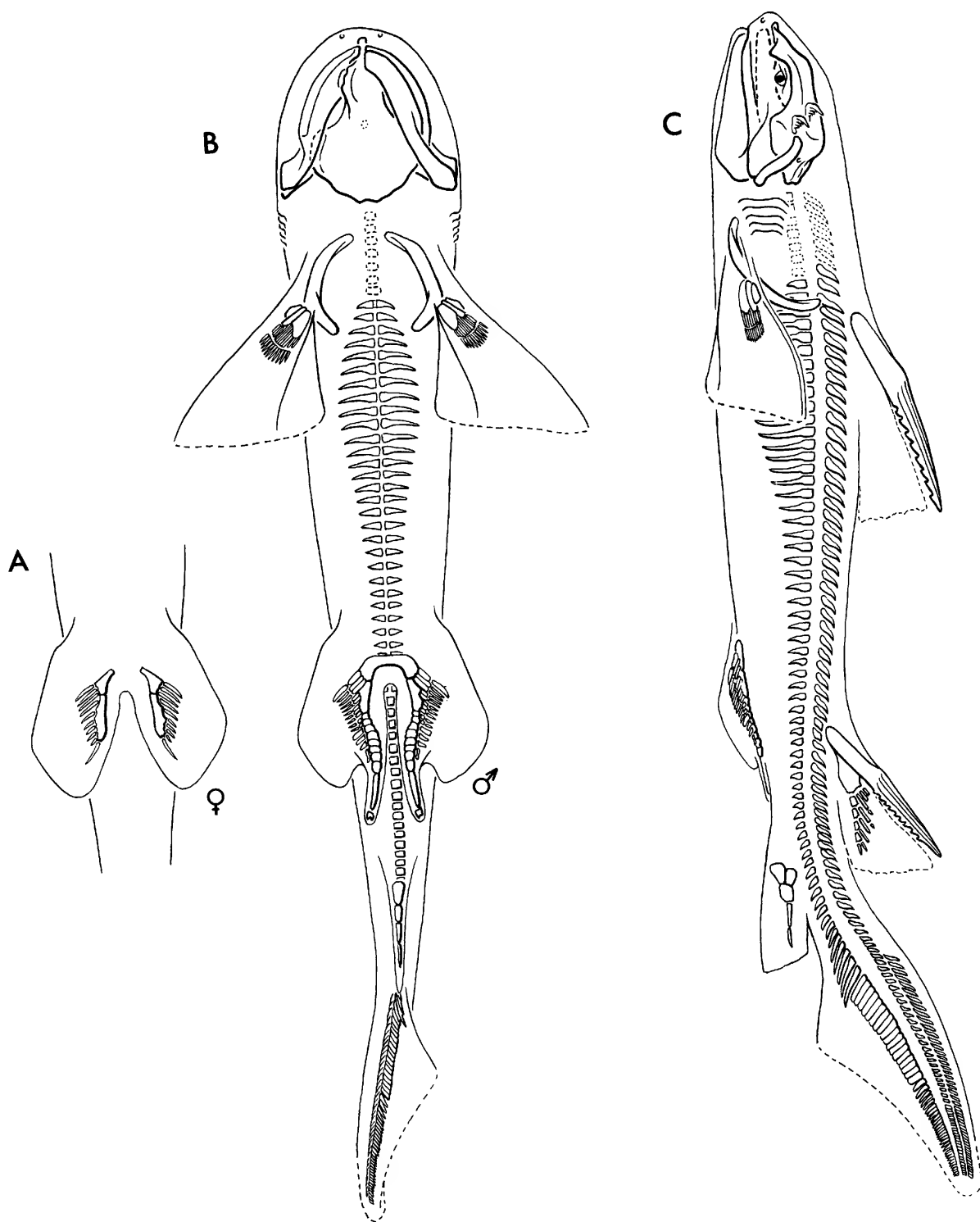


Fig. 15. Full-body reconstruction of *H. mapesi*, in ventral (A, B), lateral (C), and dorsal (D) views. Female pelvic skeleton is depicted in A; male individual is shown in B, C, and D (note claspers and cephalic spines).

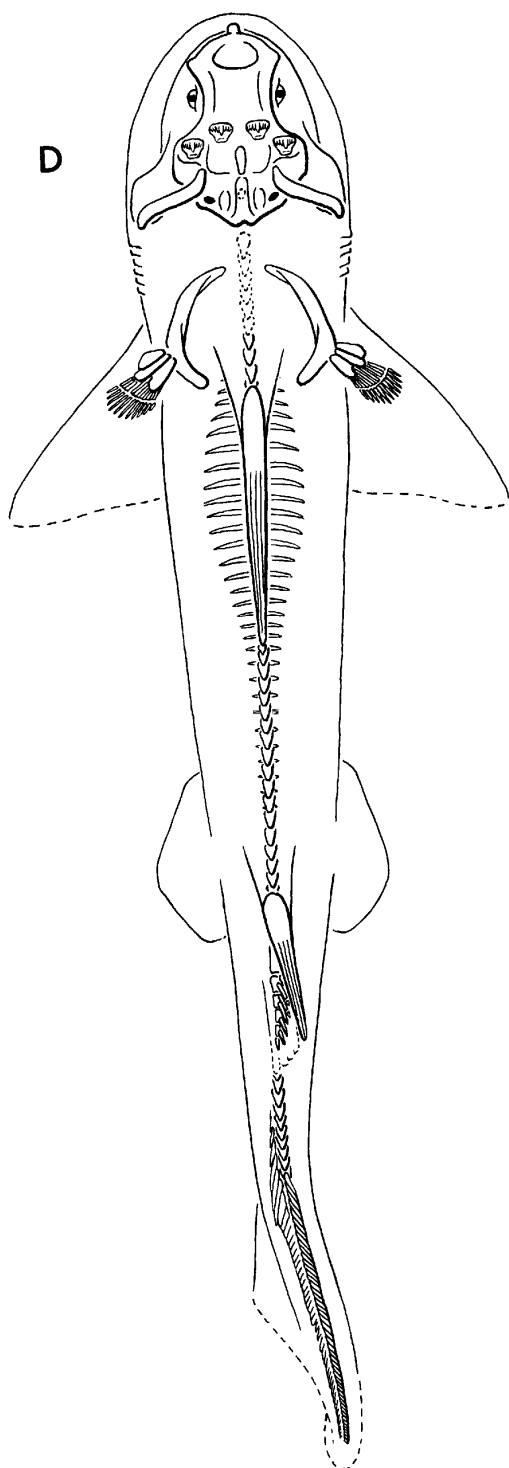


Fig. 15—Continued.

and there are seven or eight metapterygial series (fig. 14). All the mesopterygial and metapterygial radials are jointed at least once and possibly twice, and the distal radials are pointed. The proximal end of the first metapterygial radial is sandwiched between the metapterygium and propterygium, as in *Lissodus cassangensis* (Maisey, 1982: fig. 12).

The pelvic girdle and fins are well preserved in KUVF 65016, 65017, and the holotype (figs. 1–3, 16–19). In addition, parts of the pelvic clasper complex are preserved in KUVF 86305 (figs. 5, 16B). Claspers are also present in KUVF 65017 (fig. 16A), but these are lacking in the other specimens (presumed to be female).

In *Hamiltonichthys*, the female pelvic girdle clearly comprises two separate antimeres (e.g., KUVF 86308). Each half-girdle articulates with three anterior radials (fig. 19) and a basipterygial element which bears several more radials. Most of these details are confirmed by KUVF 65016, although the girdle is less clearly displayed (fig. 18B). The radials are unjointed.

In one of the male specimens (KUVF 65017), the pelvic girdle forms a continuous transverse bar, as in *Hybodus* (fig. 16A). The girdle articulates with three anterior radials and a pelvic basipterygium which bears an additional five radials (fig. 17). The basipterygium also articulates with a clasper complex, which consists of five or six radial-bearing segments, followed by three or four segments lacking radials. The first two of these are quite short, and may be regarded as the intermediate elements. The next element is slightly longer and more pointed than the others, possibly representing a submature mixipterygium (see below). Finally there is an indeterminate piece of cartilage, which could represent part of a terminal clasper complex. Most of the radials are joined in the male specimens.

UNPAIRED FINS: In the caudal fin (figs. 16, 18, 20), the neural arches are small and closely spaced, rendering the individual elements indistinct. Above this band of neural arches there are at least 50 short, unjointed epichordal fin supports. It cannot be determined whether a 1:1 ratio of supports and neural arches is maintained throughout the caudal fin, although this pattern occurs at the

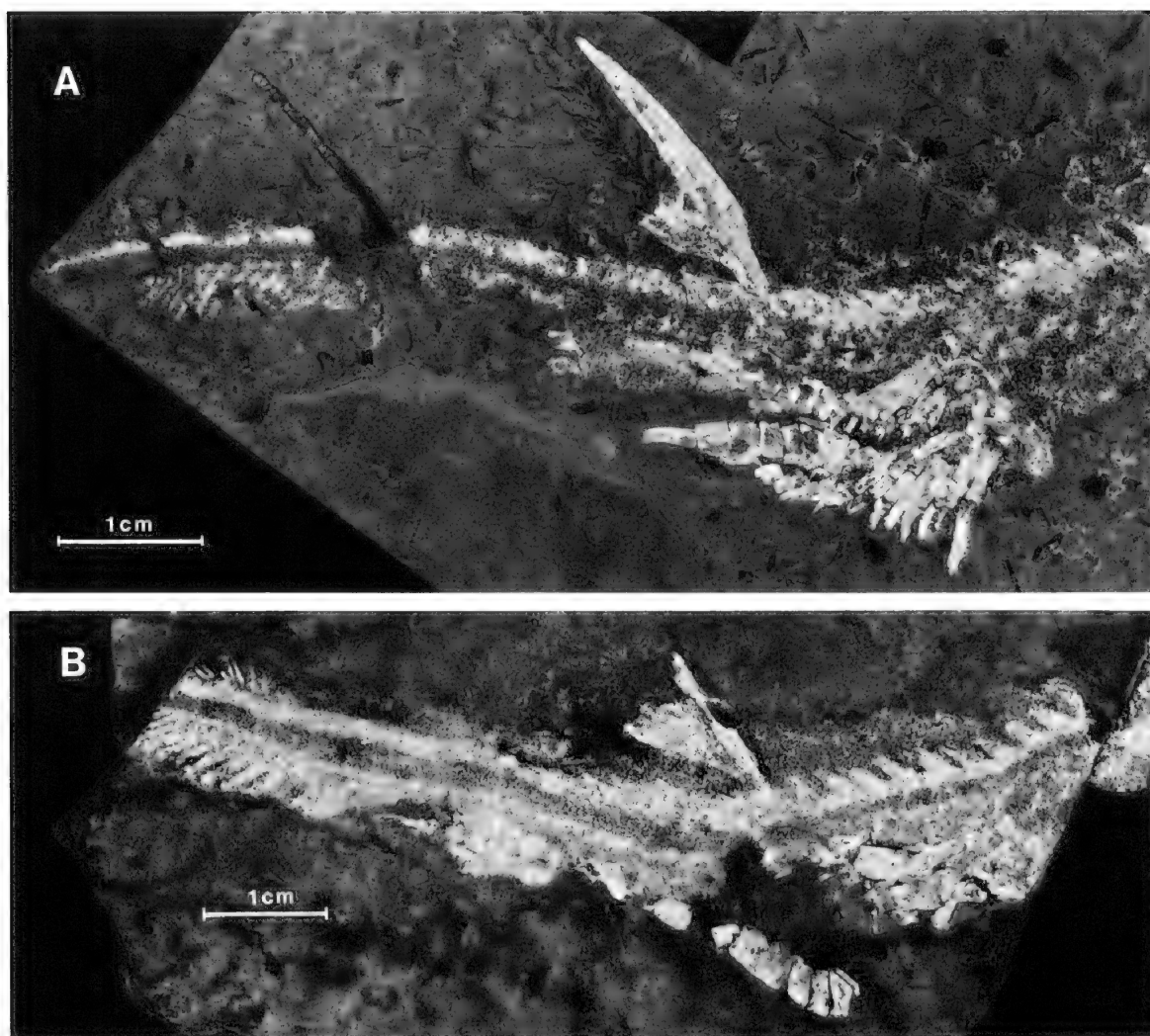


Fig. 16. Pelvic fins, second dorsal and caudal skeleton of two male *H. mapesi* specimens. A, KUVP 65017; B, KUVP 86305. UV fluorescent image. See figure 17 for explanation of pelvic fin morphology.

peduncle. Ventrally, the hypochordal endoskeleton involves some eight or nine segments anterior to the first epichordal fin support (i.e., almost 60 hypochordal arcualia are present), and the longest hypochordal fin supports occur opposite the first in the epichordal series. None of the hypochordal fin supports is jointed. As in the case of the epichordal series, the anteriormost hypochordals are arranged in a 1:1 ratio with separate hemal elements. The latter are uncalcified at the caudal extremity, however, so their segmental arrangement cannot be followed throughout the tail.

In the present work, the term “fin-support”

is used in preference to “basal” or “radial” of other authors, in referring to the caudal endoskeleton, so as to avoid implied homology or homonymy of these and other fin elements. According to Zangerl (1981: 33): “the neural arch elements may be fringed by cartilage rodlets that are homonomous with the basal rods of the dorsal; rarely, elements homonomous with the radials of the dorsal fins are also present, for example, in *Cobelodus* where three rows of cartilaginous rods are seen dorsal to the notochordal space.”

In *Falcatus*, a Paleozoic chondrichthyan morphologically very similar to *Cobelodus*, Lund (1985: 11, fig. 16) recognized discrete

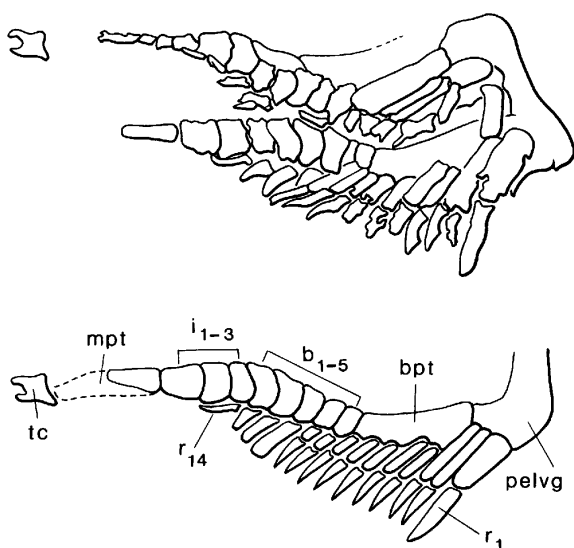


Fig. 17. Outline rendering of pelvic skeleton in KUV 65017 (above), and reconstruction of male fin and clasper complex (below), based on KUV 65017 and 86305 (see fig. 16). Note that pelvis forms a continuous transverse bar, and that the clasper axis is short (possibly indicating immaturity). Note that figures 16 and 17 are not to scale.

hypochordal “basals” between the hemal arches and ventral “radials” only in the caudal peduncle. Farther posteriorly, the hemal elements articulate directly with the “radials.” Dorsally, the neural arches are said to support both “basals” and “radials,” although the arrangement is indistinct posteriorly. The distinction between caudal “basals” and “radials” in fossil chondrichthyan thus seems to be somewhat arbitrary.

The anal fin of *Hamiltonichthys* is supported by a series of large basal plates, plus a posterior “axial” series of two or three elements (fig. 21). A complex basal series of large elements also occurs in the anal fin of *Hybodus hauffianus* (Koken, 1907; Maisey, 1982), *Diplodosselache* (Dick, 1981), *Onychoselache*, and *Tristychius* (Dick, 1978; Dick and Maisey, 1980), as well as in Recent *Heterodontus* (Koken, 1907; Smith, 1942).

There are two dorsal fins in *Hamiltonichthys*, each with a fin-spine (figs. 22, 23). The endoskeleton is extensively calcified in the posterior dorsal fin, but calcification of the anterior dorsal endoskeleton is confined to a small area just behind the fin-spine. The

following description therefore refers to the posterior dorsal fin.

There is a single triangular basal cartilage. At its deepest point this element almost meets the dorsal arcualia of the vertebral column. There is no evidence of calcified cartilaginous plates anterior to the basal cartilage as in *Squalus*, *Squatina*, or *Pristiophorus* (see Holmgren, 1941: 89 et seq., for references). Extending posteriorly from the basal cartilage is an axis of four elements, very reminiscent of a pectoral metapterygial axis (fig. 23). Each axial element usually articulates with a single preaxial radial, as well as the next axial piece. In addition there are at least three preaxial radials which articulate directly with the triangular basal cartilage. In KU 86308 (fig. 22A), however, the first axial element differs slightly in that it apparently articulates with two radials, the anteriormost of which meets the basal in other specimens (e.g., KUV 65016; fig. 22B, C).

The anterior fin-spine is inserted at approximately 40–45° to the axis of the vertebral column, whereas the posterior one is more erect (approx. 70° in KUV 86304, 86305, 86308, 65016, and 65017), an apparently plesiomorphic condition among elasmobranchs (Maisey, 1984a).

TEETH. In KUV 65016A the left upper dentition is best represented (figs. 26, 27). The most obvious dentitional landmark is a single family of elongate teeth, followed by a single series of shorter posterior lateral teeth. In KUV 86307 an elongate lateral tooth approximately 6 mm long is exposed, behind which is a single smaller tooth (fig. 8). Anteriorly there are six more tooth families in the upper dentition. The anteriormost family is parasymphyseal, with a corresponding family positioned on the opposite palatoquadrate. Between the parasymphyseal families is a single lower tooth, presumed to occupy a symphyseal position. In KUV 86304 and the holotype (figs. 9, 24, 25, 30), the elongate lateral tooth family is again present. Three upper and lower tooth families are seen in their occlusal relationship on a broken surface in the holotype (fig. 9). Only lower tooth families are exposed in KUV 86304, but this specimen confirms the presence of a single tooth family behind the longest lateral teeth (fig. 30).

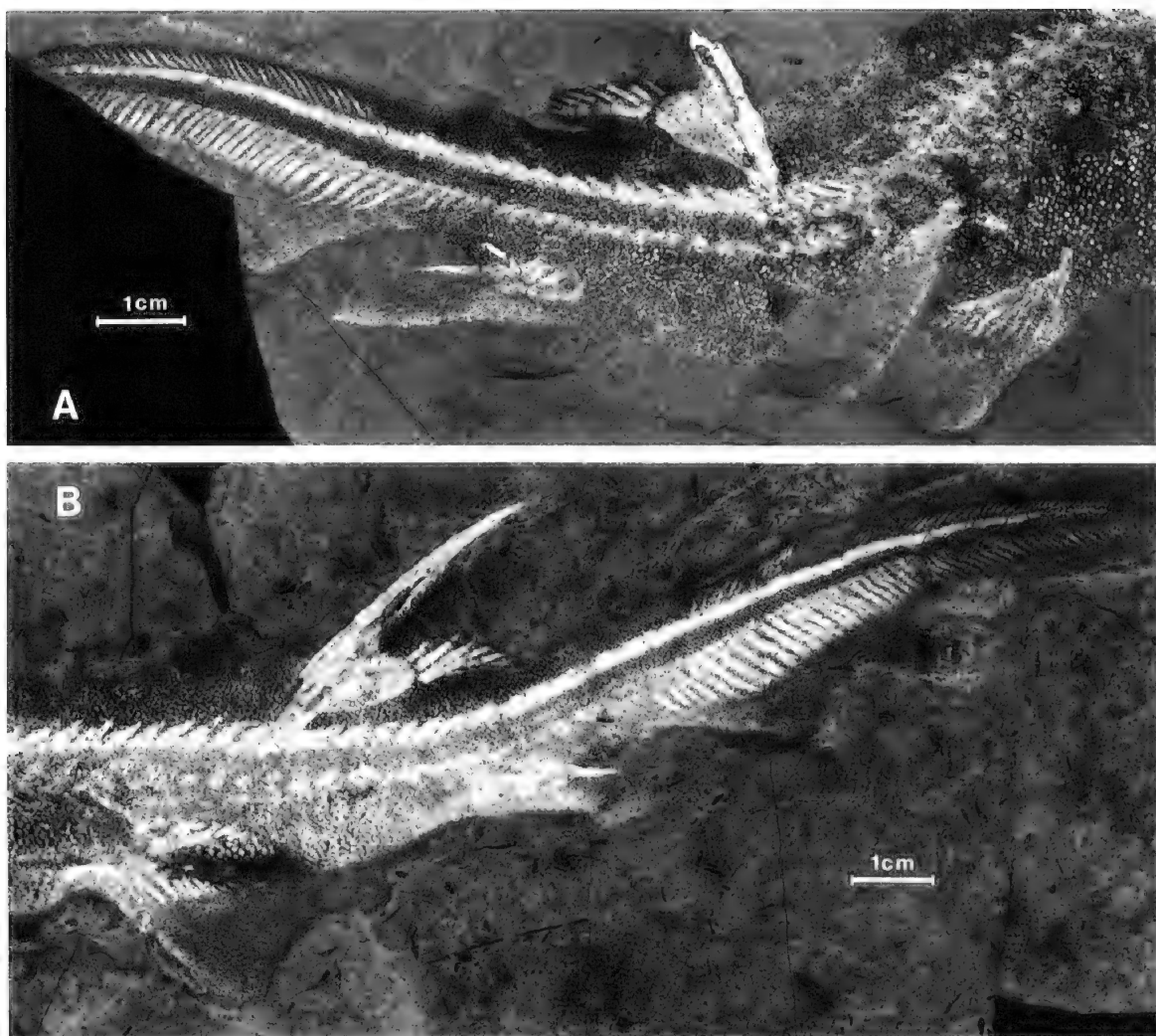


Fig. 18. Pelvic fins, second dorsal and caudal skeleton in two female *H. mapezi* specimens. A, the holotype, KUV 86308; B, KUV 65016. UV fluorescent image. See figure 19 for explanation of pelvic fin morphology.

The upper dentition of *Hamiltonichthys* therefore consists of a parasymphyseal series, followed by six families of progressively larger anterior or anterolateral teeth, a single series of very elongated teeth (approximately three times larger than in the preceding family), and a single series of upper posterior teeth. The lower dentition includes a symphyseal series, six anterior or anterolateral series, an elongate lateral series, and a single row of posterior teeth. It is possible that additional series of small posterior teeth were also present, but none have been reliably identified. There is some overlap of successional teeth in adjacent tooth families (figs.

26, 27), as in *Lissodus africanus* (discussed further below).

The teeth of *Hamiltonichthys* resemble those of *Lissodus* and *Lonchidion* in certain respects, and up to a point the descriptive terminology of Duffin (1985: 107) may conveniently be used here. The tooth crown is covered by fine vertical cristae which extend as far as the occlusal crest (figs. 24–27). This crest is straight, or else slightly angled at the highest point of the crown. Several cristae converge at the highest point, defining a cusp which is moderately elevated in the anterior teeth. This cusp is generally central, except in the elongate lateral teeth where it is located

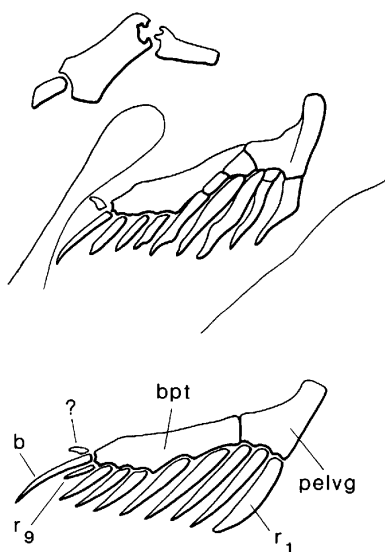


Fig. 19. Outline rendering of pelvic skeleton in KUV 86308 (above), and reconstruction of female fin (below), based on KUV 86308 and 65016 (see fig. 18). Note that pelvis consists of two separate antimeres (contrast with male specimens, fig. 17). Note that figures 18 and 19 are not to scale with each other or with figures 16 and 17.

anteriorly (fig. 25B). No lateral cusps or cusp-lets are present. The occlusal crest breaks up and becomes indistinct toward the posterior end of the longest lateral teeth (fig. 25C). Cristae are largely confined to the upper labial and lingual faces of the crown. These faces meet corresponding lower labial and lingual faces at a distinct, angular crown shoulder, which can be traced around most of the crown (fig. 25C, D).

The crown is swollen lingually, below the principal cusp (figs. 25B, 27A). The crown shoulder is continuous, but there may be a small labial "pressure scar" opposite the lin-

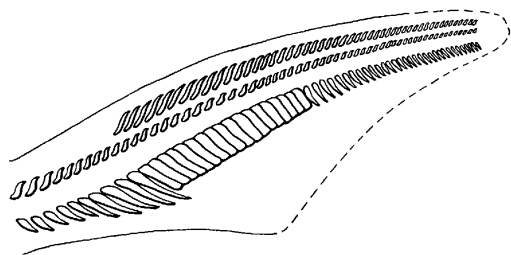


Fig. 20. Outline reconstruction of caudal endoskeleton in *H. mapesi*, based on various specimens.

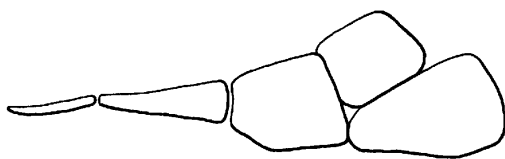


Fig. 21. Outline reconstruction of anal fin endoskeleton in *H. mapesi*, based on the holotype.

gual swelling of the preceding tooth (fig. 25C). This arrangement is apparently the reverse of that described in *Lonchidion* and *Lissodus* (Patterson, 1966; Duffin, 1985), where there is a supposedly labial peg and a corresponding lingual "pressure scar."

Most of the teeth discussed by Patterson (1966) and Duffin (1985) are isolated examples. Only in *Lissodus africanus* is the dentition reasonably well documented. Even here, however, there is some uncertainty as to tooth orientation. In the example figured by Brough (1935: pl. 2), in which upper and lower teeth are present, it cannot be determined whether the left or right teeth are exposed. In the first case, the swollen coronal peg is lingual (as in *Hamiltonichthys*). In the alternative case, the peg is labial (as generally supposed). In another specimen of *Lissodus africanus* (AMNH 8854), parts of the upper and lower dentition are also preserved. The lower tooth families lie within a shallow depression, which may represent the dental groove of Meckel's cartilage. In this case, the mesial surface of the right Meckel's cartilage is exposed, and the coronal peg of the contained teeth is labial.

These observations tend to confirm the presence of a labial peg on the crown of *Lissodus* (and probably *Lonchidion* spp.), but *Hamiltonichthys* demonstrates that deceptively similar teeth may in fact have an orientation opposite to that expected. Considerable care should therefore be exercised when describing the morphologies of isolated teeth where orientation is not firmly established. In *Acronemus* "the main cusp forms a bulbous lingual projection which overlaps the next inner tooth of the same tooth family" (Rieppel, 1982: 401), a possibly primitive similarity with *Hamiltonichthys*.

The tooth root is multiforaminate, but the configuration of the foramina is uncertain. There appears to be a row of small foramina

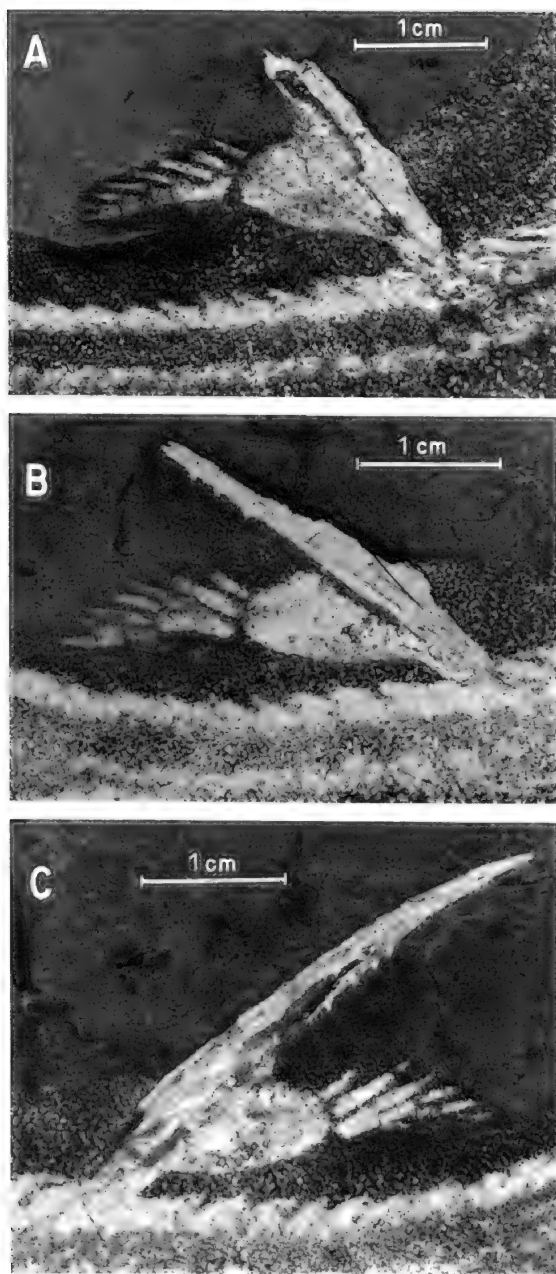


Fig. 22. Second dorsal fin endoskeleton and fin-spine in *H. mapesi*. A, the holotype (from KUVP 86308); B, C, part and counterpart of KUVP 65016. UV fluorescent image. See figure 23 for explanation.

immediately below the crown, possibly corresponding to the "foramens individuali-ees" (Casier, 1947a, 1947b, 1947c) of various Mesozoic hybodontoid teeth. The possible phylogenetic significance of such fo-

ramina has recently been reviewed elsewhere (Maisey, 1987).

SEM analysis of the teeth reveals an orthodont crown overlying the vascularized root (fig. 28), an apparently primitive arrangement among Hybodontidae (Maisey, 1987). The enameled layer is extremely thin, and apparently consists of single-crystallite enameloid (*sensu* Reif, 1973).

Four associated lateral teeth, each approximately 3.5 mm long, were found inside a small phosphatized coprolite at Hamilton

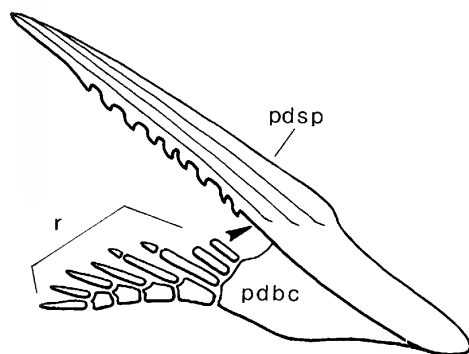


Fig. 23. Outline reconstruction of second dorsal fin and fin-spine in *H. mapesi*, based primarily on KUVP 65016 (fig. 22B, C). Arrow marks level of posterior closure in fin-spine. To scale with views in figure 22.

Quarry (KUVP 87870). Their surface ornamentation pattern is identical to that of *Hamiltonichthys*. The teeth in the coprolite evidently came from a smaller individual than is represented by complete skeletons, perhaps less than 150 mm in body length.

PHARYNGEAL DENTITION: What was initially thought to be a displaced symphyseal (mandibular) tooth-whorl in KUVP 86305 (labeled e in fig. 31A; also see fig. 33) has, following preparation of other specimens, turned out to be one of a series of presumed pharyngeal tooth-whorls, located toward the rear of the pharynx in close proximity to the scapulocoracoids (shown within boxes in figs. 9, 11; see also fig. 30). Several whorls have been found in KUVP 86304, aligned transversely across the pharyngeal region (figs. 29, 30). All the whorls are arranged with their cusps directed posteriorly, and seem to have lain in the roof of the pharynx.

These pharyngeal tooth-whorls are generally under 2 mm in diameter. Each possesses a series of cusps, ranging in number from three (fig. 29) to seven or eight (fig. 33), with the smallest at the presumed anterior end. Many of the whorls have acuminate, recurved cusps, each ornamented laterally by a single vertical ridge. Some whorls (possibly located toward the middle of the series) have short, bladelike cusps. There is considerable variation in cusp shape between adjacent whorls, although no pattern has been determined. Cusp shape is relatively consistent within each whorl, despite progressive increase in cusp size posteriorly.

It was not possible to section one of the *Hamiltonichthys* tooth-whorls, and it is therefore uncertain whether these are continuously growing structures. Certainly this is suggested by their linear cusp alignment and by the progressive increase in cusp height, but without histological evidence this cannot be confirmed. Such a growth pattern would be remarkable, since it implies the presence of an additional toothlike dental lamina within the oropharynx, posterior to the mandibular dental lamina, and capable of regular generation of new dermal papillae within presumed pharyngeal endoderm. This in turn suggests a somewhat more sophisticated inductive mechanism between pharyngeal endoderm and ectomesenchyme than has been reported in Recent elasmobranchs. An equally peculiar pattern of skeletal genome expression in early chondrichthyans is hinted at by the "extragnathal" (continuously growing?) tooth-whorls of *Falcatus* (Lund, 1985), although their rather superficial location external to the jaws suggests that they were of ectodermal rather than endodermal origin.

CEPHALIC SPINES: Cephalic spines are present in KUV 86305 and 65017 (both of which are male, according to their pelvic fin morphology). The remains of four cephalic spines have been exposed in KUV 86305, one of which is almost complete (labeled a-d in fig. 31; corresponding spines a-c are shown in fig. 32). Only one poorly preserved and morphologically uninformative spine has been identified in KUV 65017.

Two pairs of cephalic spines were present in male *Hamiltonichthys*, as in the majority of Mesozoic hybodontoids (Woodward,

1889a, 1889b; Brown, 1900; Brough, 1935; Rieppel, 1982; Maisey, 1982). The arrangement of these spines upon the head may also have been similar. Two occur together on KUV 86305A, toward the front of the head, while two others are situated farther posteriorly. Possibly this pair is homologous with the supraotic pair in *Hybodus* whereas the anterior pair was borne above the postorbital process (Maisey, 1982). The anteriorly located spines are both approximately 3 mm tall (measured from the basal plate to the upper/anterior face of the recurved principal cusp), and one is 4 mm wide (the width of the other cannot be determined). The most complete posterior spine is slightly larger (at least 3.5 mm high and 4.25 mm wide). The size differences agree with what is known of Mesozoic *Hybodus* cephalic spines, in which the posterior (supraotic) pair is the larger (e.g., Woodward, 1889a: pl. 8, fig. 1; Maisey 1982, 1987).

The cephalic spines of *Hamiltonichthys* are multicuspid, with a median principal cusp and at least three pairs of accessory or lateral cusps (fig. 32). All the cusps are acuminate and slender, but are apparently devoid of ornamentation. In section the cusps are round. The principal cusp is strongly recurved (presumably posteriorly) over the basal plate; the lateral cusps are less curved, and are progressively shorter farther laterally.

The basal plate is broad and flat, with a slightly thickened central area. There are no marginal indentations or distinct lobes. In this respect, and in cusp arrangement, *Hamiltonichthys* cephalic spines differ from most Mesozoic examples, but resemble isolated Pennsylvanian and Permian specimens (e.g., Maisey, 1982: fig. 16G, H, J, K).

Despite the presence of cephalic spines in male *Hamiltonichthys*, the clasper morphology in the two available specimens suggests a submature condition. Paradoxically, the size of the cephalic spines relative to the head is much greater in *Hamiltonichthys* than in *Hybodus*.

A few histological details can be inferred, although none of the *Hamiltonichthys* cephalic spines was sectioned. The basal plate is composed of spongy tissue. The principal cusp (and at least the first pair of lateral cusps) has an open pulp cavity, surrounded by an

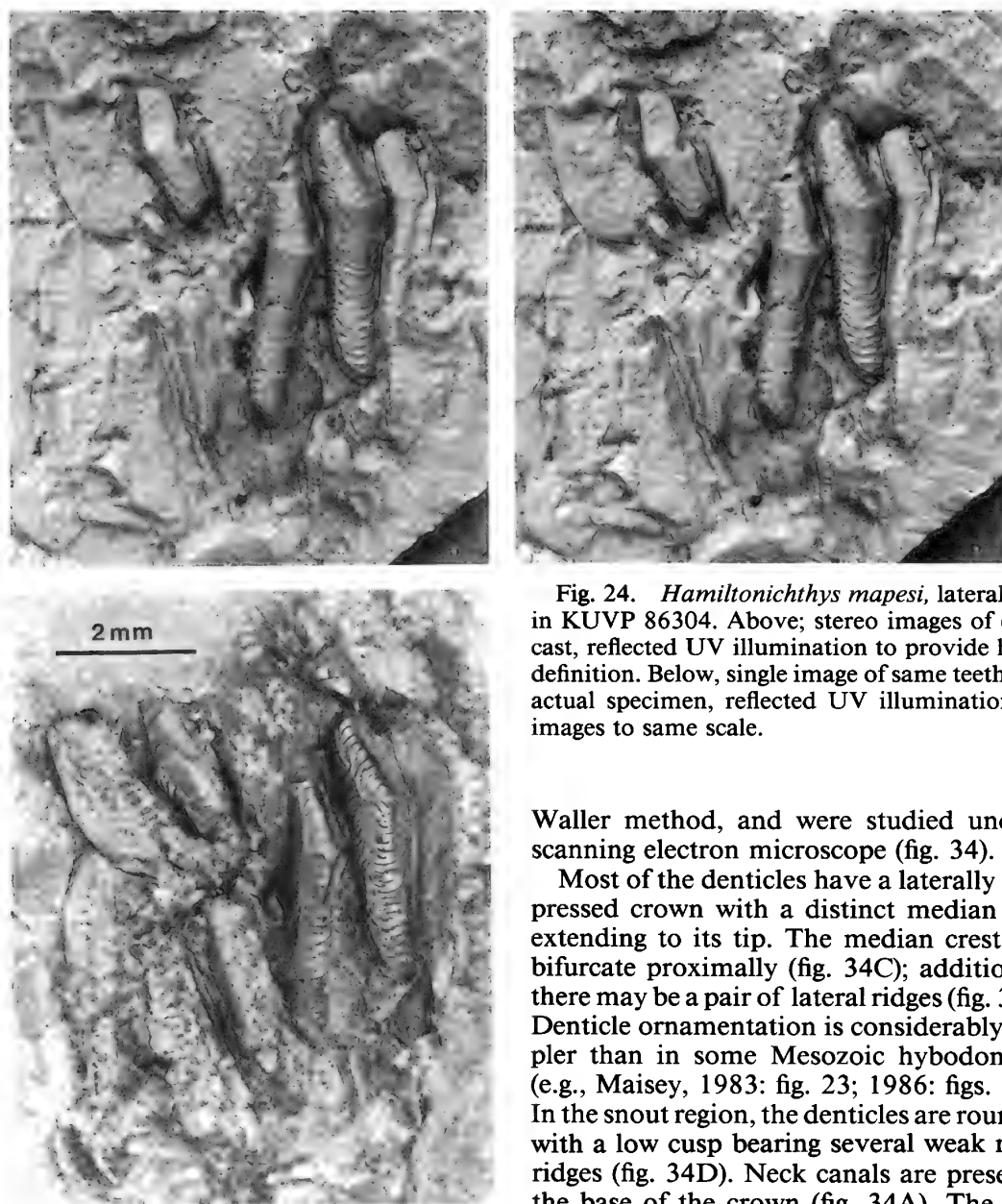


Fig. 24. *Hamiltonichthys mapesi*, lateral teeth in KUVP 86304. Above; stereo images of epoxy cast, reflected UV illumination to provide higher definition. Below, single image of same teeth from actual specimen, reflected UV illumination. All images to same scale.

unvascularized layer (of orthodentine?). The cusp surfaces are dull, and may have lacked an enameled outer layer.

DENTICLES: The body and fins of *Hamiltonichthys* are covered by a squamation of unicuspid denticles. Compound fusions of scales have not been observed. The squamation is best seen under ultraviolet light (e.g., figs. 1–6, 13, 18). Individual denticles were removed using dilute acetic acid and the

Waller method, and were studied under a scanning electron microscope (fig. 34).

Most of the denticles have a laterally compressed crown with a distinct median crest extending to its tip. The median crest may bifurcate proximally (fig. 34C); additionally there may be a pair of lateral ridges (fig. 34A). Denticle ornamentation is considerably simpler than in some Mesozoic hybodontoids (e.g., Maisey, 1983: fig. 23; 1986: figs. 6, 7). In the snout region, the denticles are rounded, with a low cusp bearing several weak radial ridges (fig. 34D). Neck canals are present at the base of the crown (fig. 34A). The basal plate (usually broken in acid-prepared denticles) is circular or weakly stellate in outline.

The position of the lateral line is sometimes indicated by a series of closely spaced denticles along each side of the presumed canal (e.g., figs. 1B, 2B, 13A). These denticles are somewhat smaller than elsewhere on the trunk, but are otherwise apparently unmodified.

DORSAL FIN-SPINES: *Hamiltonichthys* possesses two dorsal fin-spines as in *Hybodus* and many other fossil and Recent elasm-

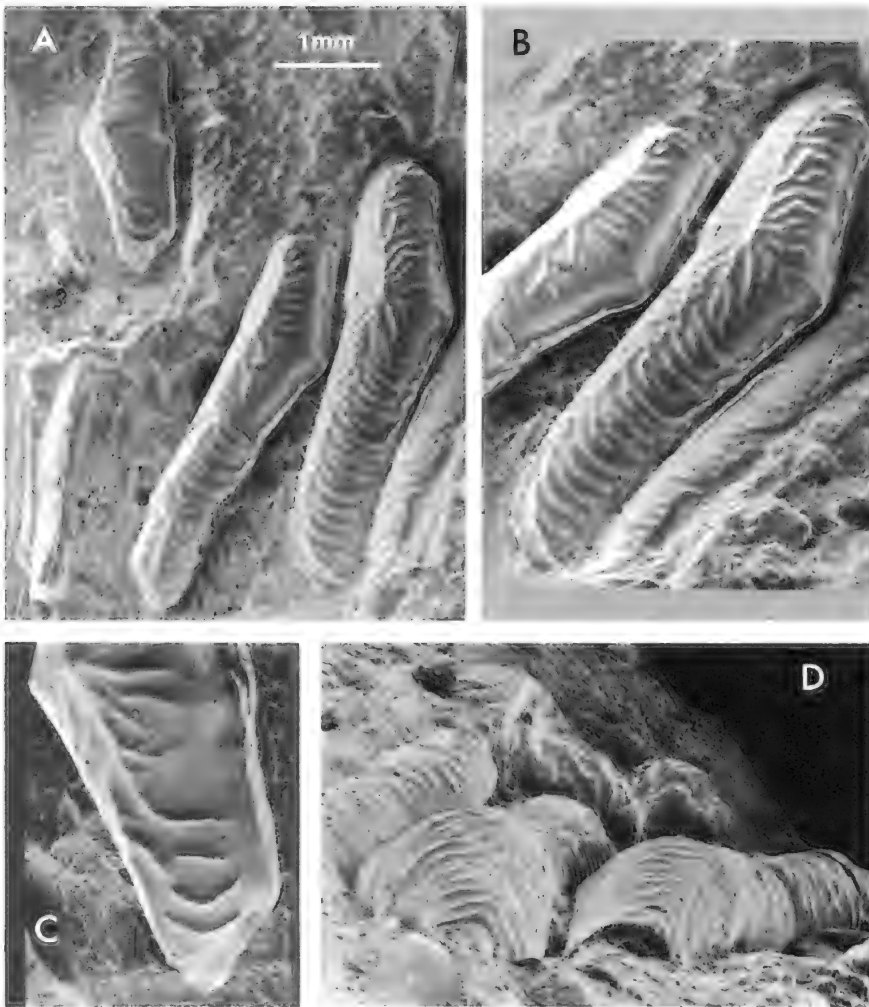


Fig. 25. *Hamiltonichthys mapesi*, lateral teeth in KUV 86304 (compare with fig. 24). Scanning electron microscope images of gold-coated epoxy cast. Scale is for A only.

branches (figs. 1–5, 15, 16, 18, 22, 23). Morphologically these fin-spines closely resemble those referred to *Hybodus*, *Acrodus*, *Palaeobates*, *Lissodus*, and *Lonchidion*. The anterior fin-spine is slightly the longer, as the following measurements (in mm) indicate:

KUV no.	Ant.	Post.	Sex
65017	29.5	23	M
65016	43	39.5	F
86304	37	30	F?
86304	52.5	—	F

Terminology used in the present account is after Maisey (1978). The fin-spines have an open pulp cavity extending almost to their tip (e.g., KUV 86304B). The posterior wall

is open proximally for about a third of the spine length (fig. 23, arrow). Above the level of posterior closure the spine bears a series of retrorse denticles, arranged alternately on either side of the midline. These denticles are poorly preserved in most cases. The anterior fin-spine of KUV 86304 has about a dozen denticles. About half this number are preserved on the incomplete posterior fin-spine of KUV 65016A.

The anterior and lateral surfaces of the fin-spines are ornamented by continuous smooth ribbing. In addition to a single rib along the leading edge (e.g., KUV 86305B, 65016B, 65017), there are no more than two or three lateral ribs. Each rib has a shiny surface, but

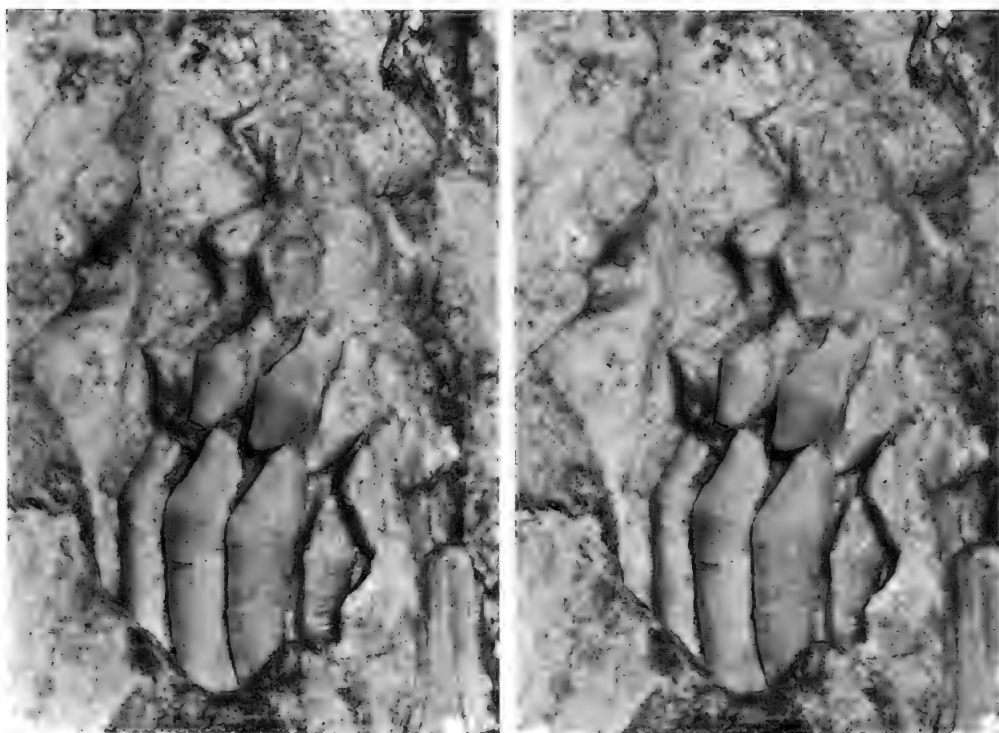


Fig. 26. *Hamiltonichthys mapei*, lateral teeth in KUVP 65016. Stereo images of actual specimen taken with combined tungsten (white light) and UV fluorescence illumination.

lacks an obvious enameled layer (i.e., as in *Hybodus* and *Acrodus*; Maisey, 1978). The shape in cross section is ovoid, and the posterior wall is convex. There is a distinct anterior "saddle," or change in profile, at the level of insertion of the posterior fin-spine (fig. 22, 23), but the anterior fin-spine lacks a saddle, confirming the view that hybodontid posterior fin-spines may be identified by the presence of a saddle (Maisey, 1974, 1978).

DISCUSSION

PALEOBIOLOGY OF *HAMILTONICHTHYS*

Certain aspects of *Hamiltonichthys* skeletal anatomy collectively suggest that only sub-mature individuals are represented at the Hamilton Quarry locality. When this is considered in the light of the supposed paleoenvironment in which these sediments were deposited, some tentative statements may be made concerning the mode of life of *Hamiltonichthys*. It must be stressed, however, that these remarks are highly speculative and difficult or impossible to confirm (see also Maisey, 1988).

All of the complete specimens of *Hamiltonichthys mapei* are small, none exceeding 300 mm total length. Only the isolated caudal fin (KUVP 88641) may have come from a somewhat larger individual. Male specimens possess cephalic spines and a well-developed clasper complex, although the axial mixipterygial cartilage is relatively shorter than in *Lissodus cassangensis* or *Hybodus hauffianus* (see Maisey, 1982: fig. 13), and a terminal clasper complex is not preserved. This raises the possibility that the *Hamiltonichthys* specimens are immature or submature, like the majority of *Acanthodes* from Hamilton (Zidek, 1976). Differences in male and female pelvic girdle morphology (cf. figs. 17, 19) might then be of ontogenetic significance.

Although adult clasper morphology of Recent chondrichthyans is well documented, ontogenetic data are sparse. Thorson's (1983) investigation of a euryhaline stingray, *Dasyatis guttata*, has revealed that there is a burst of rapid clasper growth during sexual maturation, around 500 mm disc width. Clasper length increases dramatically, from between 5 and 10 percent of disc width, to over 20

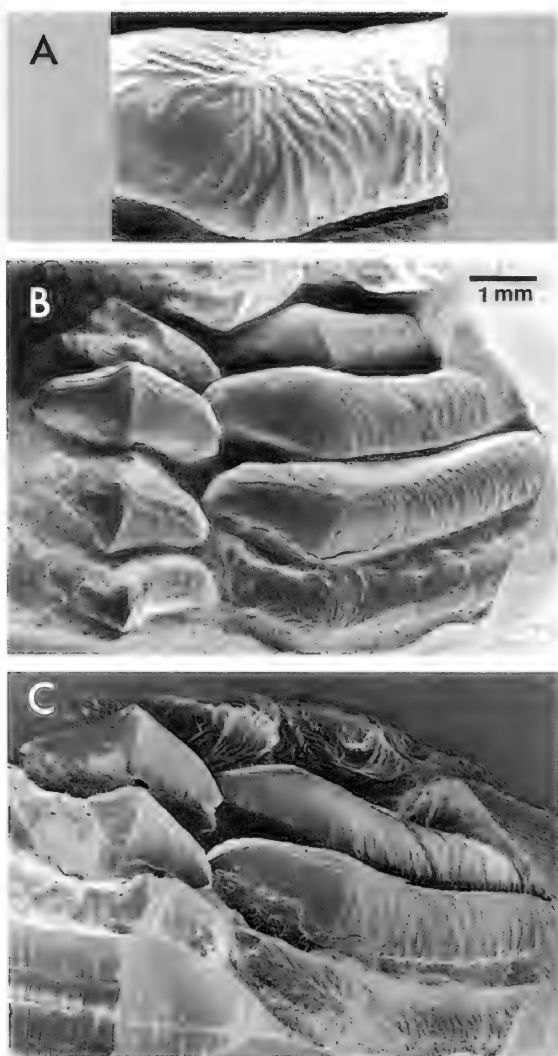


Fig. 27. *Hamiltonichthys mapesi*, lateral teeth in KUVF 65016 (compare with fig. 26). Scanning electron microscope images of gold-coated epoxy cast. Scale is for B only.

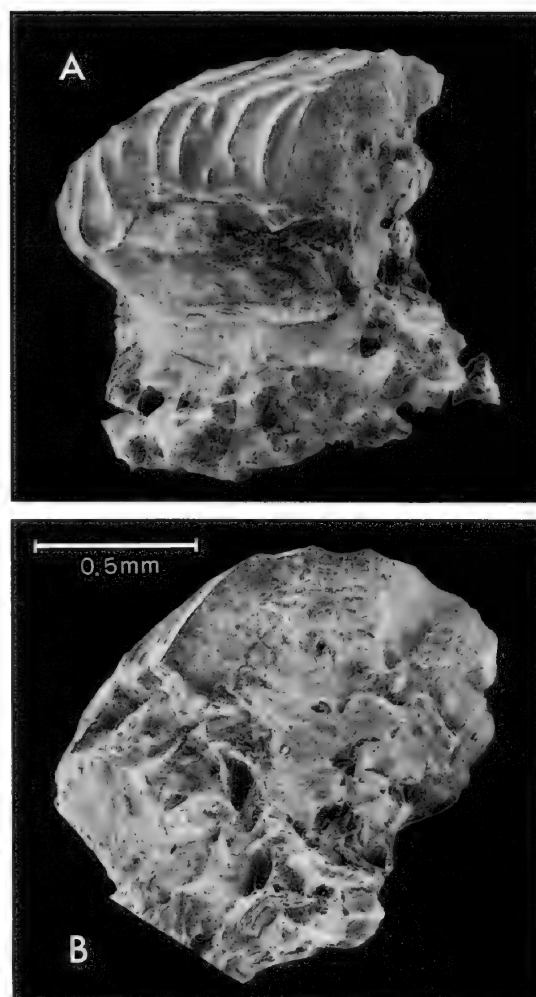


Fig. 28. *Hamiltonichthys mapesi*, holotype, AMNH 10708. Scanning electron microscope images of incomplete lateral tooth. A, oblique labial view, showing coronal wrinkles; B, view of broken surface, showing orthodontine crown and vascularized root. Tooth prepared using Waller method.

percent. Capapé (1985) has documented similar clasper growth patterns in several genera of Recent sharks, skates, and rays.

My own anatomical comparisons of cleared and stained juvenile and adult *Chlamydoselachus*, *Squalus*, *Squatina*, *Pristiophorus*, and *Mustelus* suggest that the axial, Beta, and intercalary cartilages are chondrified at an early stage, but that the terminal clasper complex chondrifies somewhat later. Furthermore, the axial cartilage is generally thin and spindly in juveniles, and is relatively shorter than in the mature adult. In none of the *Ham-*

iltonichthys material where the claspers are preserved can a terminal clasper complex be discerned, unlike in *Lissodus cassangensis* and *Hybodus hauffianus* (Maisey, 1982). The shortness of the axial cartilage, together with the absence of a terminal clasper complex in the Kansas hybodonts, suggests that these are submature individuals, but the prominent cephalic spines of males suggest impending sexual maturity.

Calcification of the braincase floor around the hypophyseal fossa, and of the *tectum antoticum*, suggests that cranial development

was essentially complete by the 300 mm stage. These areas are among the last to chondrify in Recent elasmobranch embryos (de Beer, 1931, 1937; Holmgren, 1940). By the time *Hamiltonichthys* reached a length of 300 mm, it possessed essentially adult dentition, squamation, and fin-spines (plus cephalic spines in males).

Among Recent elasmobranchs, few taxa attain sexual maturity at such a small size (e.g., *Etmopterus* spp.; Bigelow and Schroeder, 1948). *Lissodus cassangensis* nevertheless apparently reached maturity at approximately 150 mm total length (Teixeira, 1954, 1956; Maisey, 1982). Most *Lissodus africanus* specimens are not longer than 200–300 mm (Broom, 1909; Brough, 1935). It is quite possible that, because of some physiological, ecological, or preservational factors, only small individuals have been preserved in the fossil examples cited above (as seems to be the case for Hamilton *Acanthodes*; Zidek, 1976).

In this regard, Thorson's (1983) study of *Dasyatis guttata* is again of interest. Parturition in this species typically occurs in inland waters with very low salinity, between 0 and 5 parts per thousand (ppt). The neonate sting-rays soon migrate downstream to waters of higher salinity (20 ppt). During maturation the males can tolerate very high salinities, even full-strength seawater, but after maturation they migrate back upstream and re-enter freshwater, along with the maturing females. The latter become confined to these waters and can only tolerate salinities of up to 4 ppt, where they may attain great size (up to 30 kg weight and 1 m disc width).

Extending this analogy to *Hamiltonichthys*, the available specimens could represent a submature population which was in the process of migrating downstream, from a low-salinity parturition site (in which larger adults were perhaps confined), to a more saline environment (where the new generation might reach maturity). This is an admittedly elaborate scenario (Maisey, 1988), but is worth exploring since there is a modern precedent, and some Mesozoic hybodontoids may also have been euryhaline (e.g., *Egertonodus*

basanus; Maisey, 1983). According to Duffin (1985), *Lissodus* includes many marine and freshwater species, although it is not known whether particular taxa were euryhaline. Whatever the case, there is a distinct possibility that many hybodontoid species were partly or fully euryhaline.

It is noteworthy that the Hamilton Quarry locality has yielded other supposedly juvenile fossil vertebrates, including many small specimens of *Acanthodes bridgei* (Zidek, 1976, 1988), palaeoniscoids (Gottfried, 1988), disorophoid amphibians (Daly, 1988), and a

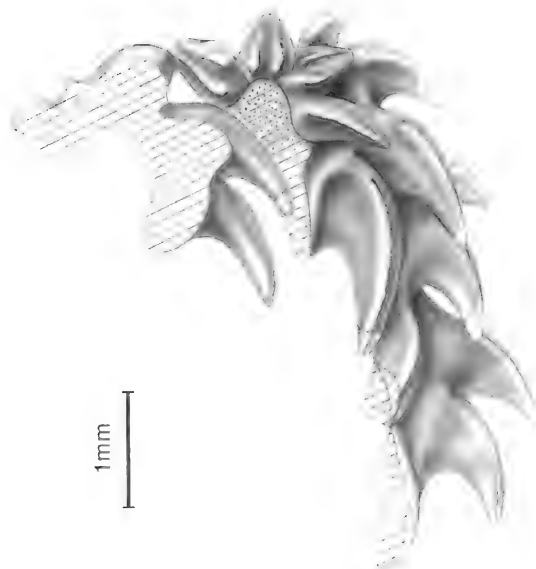


Fig. 29. *Hamiltonichthys mapesi*, KUPV 86304, pharyngeal tooth-whorl complex. Pencil rendering viewed from same orientation as photo in figure 30.

juvenile diapsid reptile (Reisz, 1988). Larger, presumably more mature vertebrates are somewhat rare, and are represented by xenacanth (including one or two large, isolated teeth; Schultz and Chorn, 1988), the dipnoan *Sagenodus* (Chorn and Schultze, 1988), an osteolepidid (Schultze, 1988), and a diapsid tetrapod (Reisz, 1988). The Hamilton biota thus appears to be biased toward juvenile vertebrates, which could be accounted



Fig. 30. *Hamiltonichthys mapesi*, KUV 86304, head region showing dentitional teeth and pharyngeal tooth-whorl complex (compare with fig. 29). UV fluorescent image.

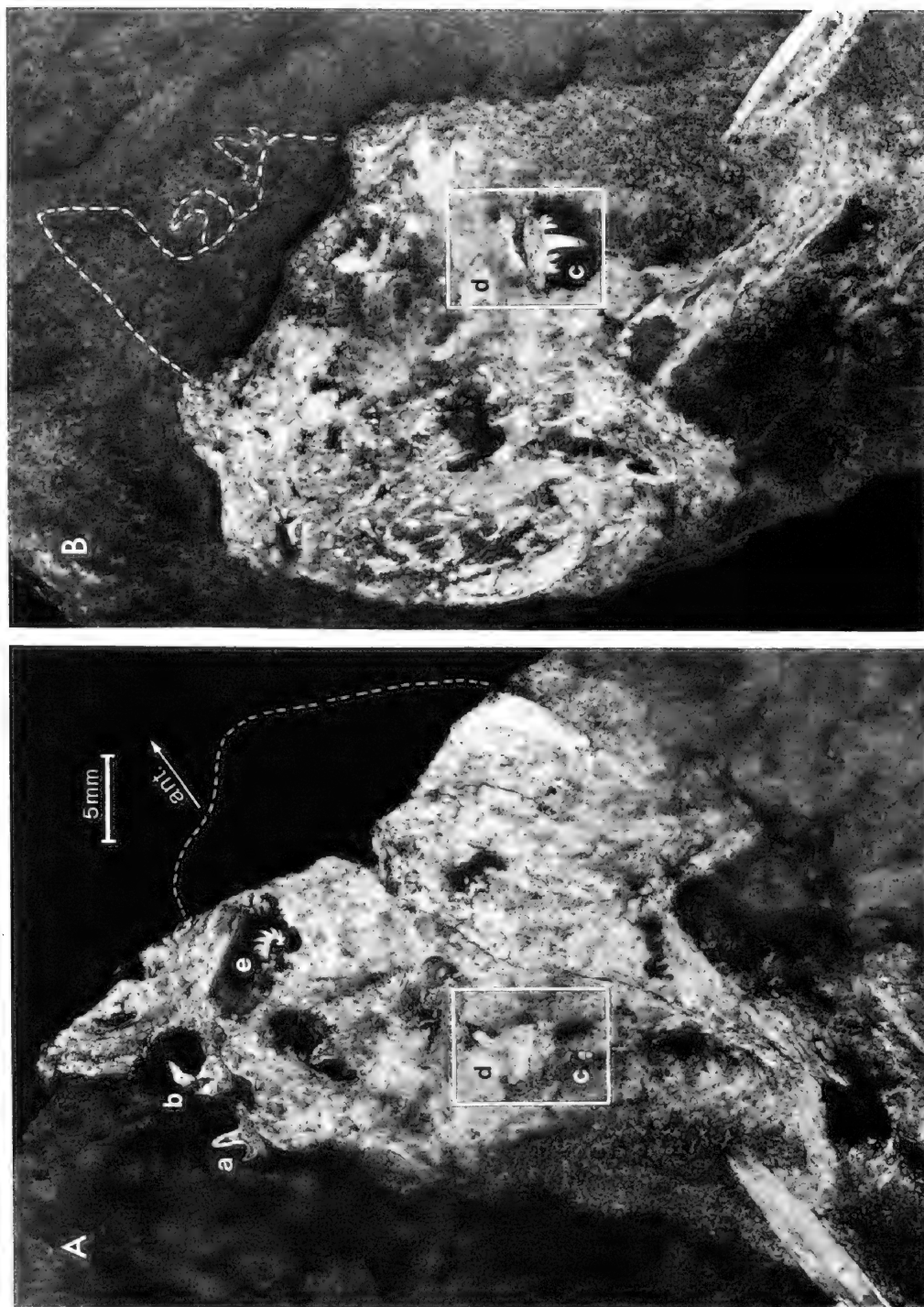


Fig. 31. *Hamiltonichthys mapei*, KUV 86305, head region of male specimen in part and counterpart. Views are oriented as mirror-images, but outlines seem to differ because various parts are missing. To facilitate comparison, dashed lines represent "missing" areas on the opposite half. In view A, parts of four cephalic spines (a-d) and a pharyngeal tooth-whorl (e) are exposed. In view B, parts of two cephalic spines (c, d) are evident (boxed in both views). Arrow in A points in direction of snout. UV fluorescent image.

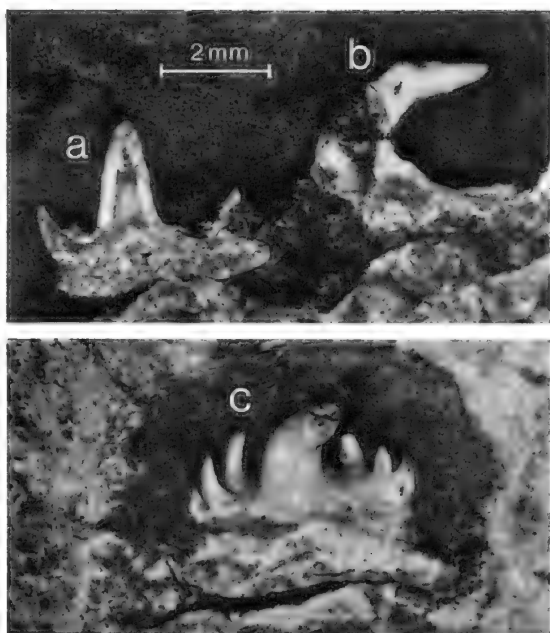


Fig. 32. *Hamiltonichthys mapesti*, KUV 86305, three of four cephalic spines from male individual, designated a–c as in figure 31. Spine (a) is broken through transversely, revealing a large pulp cavity in each cusp. Spine (b) is sliced tangentially, but the principal cusp (viewed from left side) is intact. Cephalic spine (c) has been excavated and is seen in posterior view; the tip of the principal cusp is missing, revealing a pulp cavity. Views are to scale. Combined tungsten (white light) and UV fluorescent images.

for by any number of ecological and taphonomic factors. It is hoped that future sedimentological and paleoecological investigations at this important site will shed further light upon the causes of this remarkable occurrence.

PHYLOGENETIC RELATIONSHIPS

A detailed investigation of all the morphological data now available for hybodontiform elasmobranchs is being prepared for publication, and consequently only a few remarks concerning the phylogenetic position of *Hamiltonichthys* will be made here.

Elsewhere I have advanced the hypothesis that certain well-known Mesozoic hybodontids (*Hybodus*, *Acrodus*, *Egertonodus*, *Asteracanthus*, *Palaeobates*, and perhaps *Bdellosodus*) form a monophyletic group. Within that

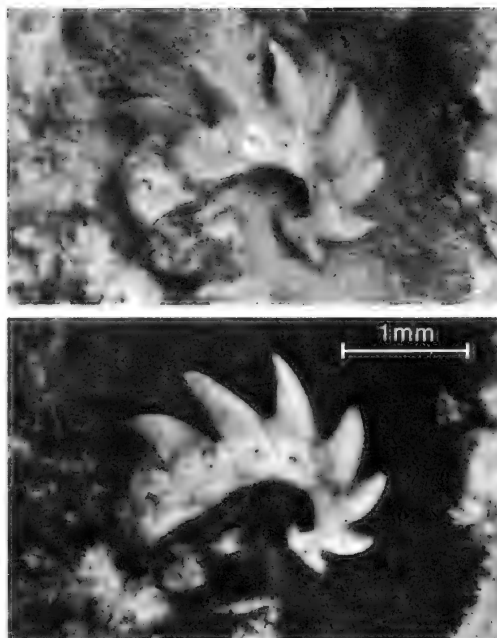


Fig. 33. *Hamiltonichthys mapesti*, KUV 86305. Single pharyngeal tooth-whorl (designated as e in fig. 31); tungsten (white light) image (above) and UV fluorescent image (below), to same scale. Note: scale differs from that used in figure 32.

group (Maisey, 1987), *Palaeobates* was considered to be the most plesiomorphic member. I also suggested that *Hybodus* and *Egertonodus* formed a monophyletic group characterized by high-crowned, multicuspid, osteodont teeth. Taxa with low-crowned, tumid, osteodont teeth may form another monophyletic group, although the data presented were equivocal.

Cappetta (1987) subdivided these taxa similarly, but on a phenetic basis. He also recognized a third group (his Polyacrodontidae) to include *Polyacrodus*, *Lissodus*, *Lonchidion*, and (tentatively) *Palaeobates*. The validity of the Polyacrodontidae will not be debated here, but as defined by Cappetta (1987) the group is probably founded upon plesiomorphic characters (Patterson, 1966; Maisey, 1987).

These Mesozoic taxa are not all known in equivalent detail, and the distribution of certain critical characters needs to be better determined. Nevertheless, it appears that *Hamiltonichthys* differs from many, if not all, of them in several features, including:

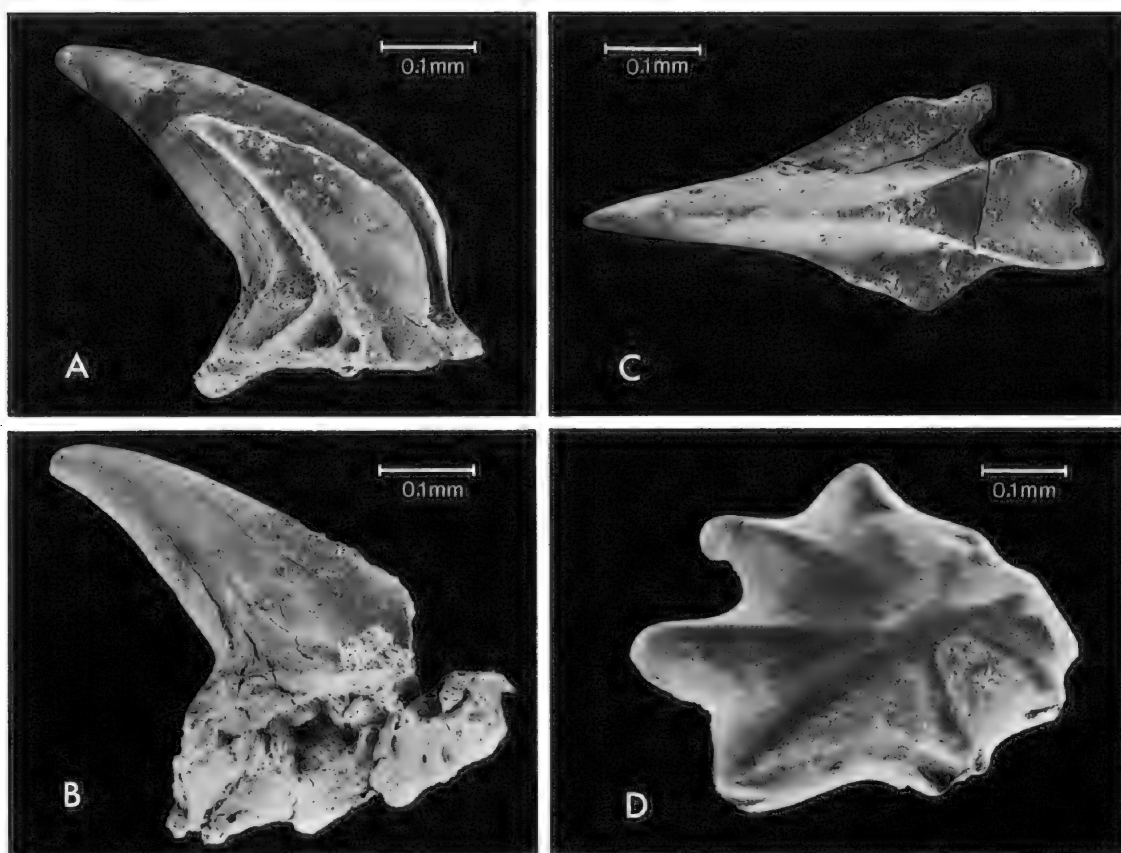


Fig. 34. *Hamiltonichthys mapei*, scanning electron microscope images of isolated dermal denticles, removed from matrix using the Waller method, and then gold-coated. A–C from trunk region of KUV 65016; D from snout of holotype, KUV 86308. Note that A–C are different denticles, not different views of same denticle. Using Tway and Zidek designations, denticles A and B are subtype 229; C is subtype 062; D is subtype 140.

- (a) no puboischiadic bar in females
- (b) palatoquadrate has only an anteromesial ethmoidal articulation with the braincase, lacking a more dorsal (ethmopalatine) one, and the quadrate moiety is curved laterally away from the braincase, not sliding beneath the postorbital process
- (c) hyomandibular orientation
- (d) “hybodontid-type” growing dermal denticles absent
- (e) cephalic spines lack triradiate base morphology, retain large lateral cusps
- (f) coracoid region shorter than scapular one

Hamiltonichthys is thus a cladistically primitive genus in comparison with most Mesozoic hybodontids, although it shares the following characters with them:

- 1. Pectoral basal and radial configuration
- 2. Low number (10–12) paired pleural ribs
- 3. Convex fin-spine posterior wall with retorse, alternating denticle rows
- 4. Cephalic spines
- 5. Puboischiadic bar
- 6. Large, downturned postorbital process
- 7. Inflated, elongate jugular canal
- 8. Postorbital articulation absent
- 9. Otic capsules between postorbital processes

This list provides compelling evidence that *Hamiltonichthys* is a hybodontoid, albeit a cladistically primitive one. It is therefore regarded here as a sister-taxon to the better-known (mainly Mesozoic) hybodontoids.

Taking all these taxa and comparing them with other putative Paleozoic “hybodonts”

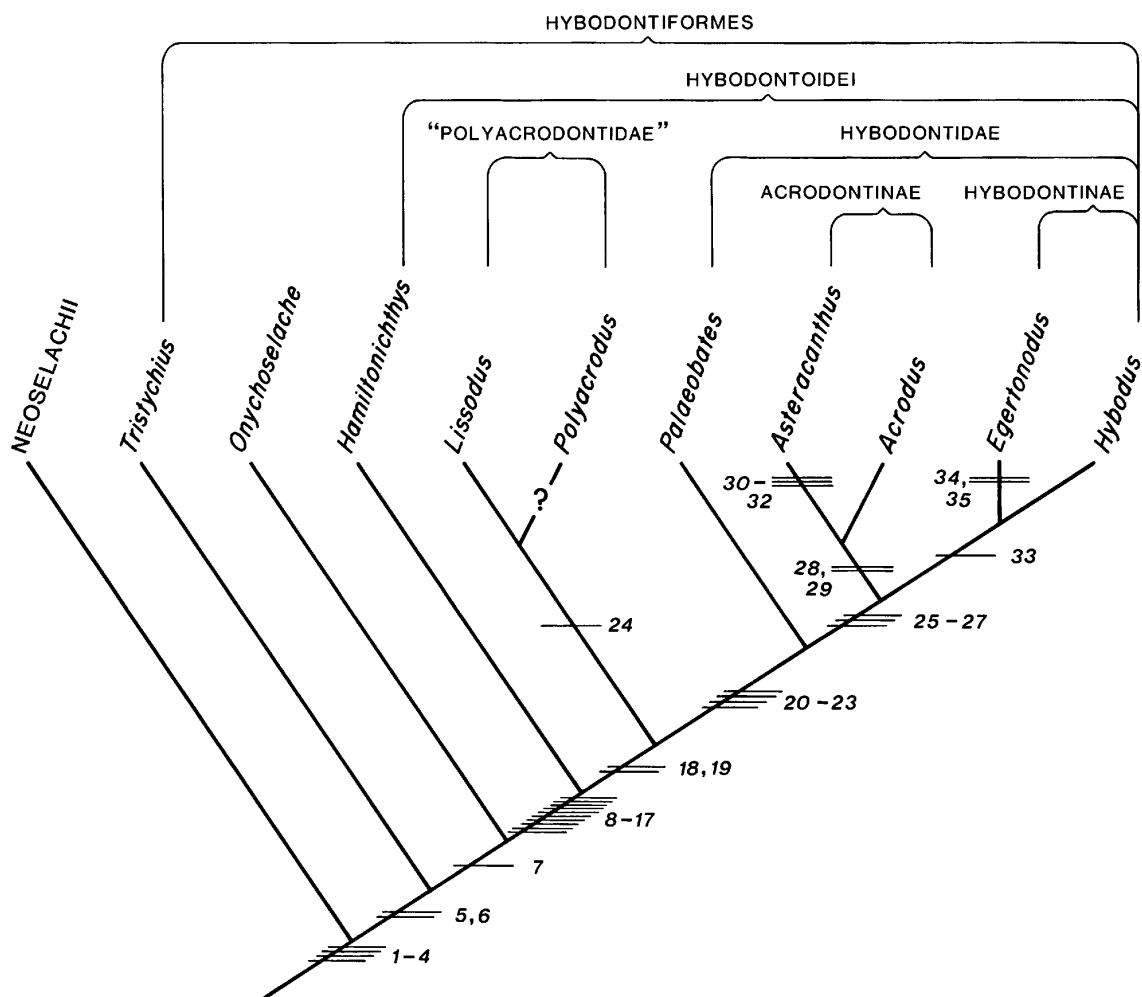


Fig. 35. Hypothesis of phylogenetic relationships among the better-known fossil Hybodontiformes. Nodes on the cladogram are defended by the following characters: 1, shoulder-joint with strong propterygial support; 2, pectoral articulation rotated; 3, enlarged pelvic "propterygium"; 4, glossopharyngeal canal; 5, calcified pleural ribs; 6, fin-spines possess large retrorse denticles and smooth ribs; 7, low-crowned teeth; 8, otic capsules located between postorbital processes; 9, elongate lateral teeth; 10, postorbital articulation absent; 11, inflated and elongate jugular canal; 12, large, downturned postorbital process; 13, puboischiadic bar in males; 14, cephalic spines present; 15, fin-spines have convex posterior wall, denticles adjacent to posterior midline; 16, low number (10–12) of pleural ribs; 17, pattern of pectoral basals and radials; 18, coracoid and scapular regions of subequal length; 19, puboischiadic bar in females; 20, palatoquadrate with separate ethmopalatine and ethmoidal articular surfaces anteriorly; 21, erect hyomandibula with broad upper end passing dorsal to palatoquadrate; 22, "hybodontid-type" growing dermal denticles (sensu Reif); 23, "*Sphenonchus*" cephalic spines; 24, "convict arrow"-shaped cephalic spines; 25, osteodont teeth with anaulacorhize base; 26, cephalic spines with secondarily closed pulp cavity; 27, large labial apparatus; 28, teeth with columnar osteodentine; 29, adjacent tooth-rows; 30, fin-spines with stellate tubercles; 31, cephalic spines lack accessory cusps; 32, elaborate durophagous dentition and specially braced mandibular cartilages; 33, high-crowned, multicuspid teeth; 34, all dermal denticles nongrowing; 35, single pair of cephalic spines.

such as *Tristychius* and *Onychoselache* leads to the conclusion that all of them share elongate calcified pleural ribs and fin-spines with large retrorse denticles posteriorly and smooth

costal ornament anteriorly, which may represent synapomorphies (fig. 35). Additionally, *Onychoselache* apparently possesses small tooth-whorls like those of *Hamilton-*

ichthys, although their arrangement and location within *Onychoselache* has not been determined. The evidence that *Tristychius* or *Onychoselache* are related to hybodontoids is therefore weak, but some contrary evidence (e.g., from their cladistically primitive unfused pelvic half-girdles) is shown by *Hamiltonichthys* to be inadmissible. *Hamiltonichthys* seems to refute the hypothesis that the fused puboischadic bar is a synapomorphy of hybodontoids and Recent elasmobranchs (Compagno, 1973). Further data are required in this regard from cladistically primitive neoselachians such as *Hopleacanthus* (see Schaumburg, 1982; Maisey, 1984a).

I conclude that the ichthyofauna of the Pennsylvanian Hamilton Quarry, Kansas, includes a very early representative of the Hybodontidae, a monophyletic group of elasmobranchs which rose to dominance during the Mesozoic. This new species is considered generically distinct, and is named *Hamiltonichthys mapei*. The description is based on a hypodigm of eight specimens, all of which may be submature, according to clasper morphology in male individuals.

Comparison of *Hamiltonichthys* with other fossils allows us to develop a hypothesis of relationships among the Hybodontiformes that is open to outgroup comparison with Recent elasmobranchs. Available data have not refuted my hypothesis that those hybodontids possessing high-crowned osteodont teeth are phylogenetically advanced (Maisey, 1987). Among plesiomorphic Hybodontidae with low-crowned orthodont teeth, *Palaeobates* is perhaps closest to the osteodont group, with which it shares specialized "*Sphenonchus*" cephalic spines and some cranial characters. Resolution of relationships among putative primitive members of the Hybodontiformes (e.g., *Onychoselache*, *Tristychius*) is made harder by their phylogenetic proximity to a major divergence of the group from neoselachians (a monophyletic group comprising all Recent elasmobranchs, plus fossils such as *Palaeospinax* and *Hopleacanthus*). The phylogenetic hypothesis shown in figure 35 is based in part upon the suite of characters listed in the figure caption. Some of these characters involve as yet unpublished data for certain taxa that have not been included in this paper. Further dis-

cussion of the hypothesis and characters will appear in due course.

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